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A COMPARATIVE STUDY OF THREE SPECIES OF BITHYNIIDAE (MOLLUSCA: PROSOBRANCHIA): *PARAFOSSARULUS MANCHOURICUS*, *GABBIA MISELLA* AND *BITHYNIA TENTACULATA*

Pyung-Rim Chung

ABSTRACT

Three species of freshwater snails of the family Bithyniidae, *Parafossarulus manchouricus, Gabbia misella* and *Bithynia tentaculata*, were compared in regard to various biological characteristics and a satisfactory culture method was devised for laboratory rearing of all three species. These snails are iteroparous and lay eggs once a year. *P. manchouricus* grew to adult size in about 54 days after hatching and laid eggs 150-156 days after hatching.

The bithyniid protoconch is nearly smooth, except for small, low spiral wrinkles, a sculpture which is quite different from that of the Hydrobiidae, a family in which the bithyniids are sometimes placed.

Two different chromosome numbers were observed in the three bithyniid species: n=17 in *Parafossarulus manchouricus* and *Bithynia tentaculata*, and n=18 in *Gabbia misella*. There were morphological differences in the karyotypes of the three species, as might be expected, but also differences in the karyotypes of European and American strains of *B. tentaculata*, which was not expected. This may be additional evidence of a pre-European-settlement origin for some of the American *B. tentaculata*.

Allozyme variations between the allopatric populations of *Parafossarulus manchouricus, Gabbia misella* and *Bithynia tentaculata* were observed in glutamate-oxaloacetate transaminase, alkaline phosphatase-1, acid phosphatase-2, alanine aminopeptidase, esterase-4 and esterase-5 activities. The glutamate-oxaloacetate transaminase banding patterns were species-specific in *B. tentaculata* and population-specific in the Chongpyung (Korea) strain of *P. manchouricus*. Variability in the latter species may be related to genetics of susceptibility to *Clonorchis* infection. The electromorphs for esterase-4 activity also showed population-specific patterns for the Portuguese, German and Michigan strains of *B. tentaculata*. The allozymes encoded by alkaline phosphatase-2 and alkaline phosphatase-3 loci in *P. manchouricus* were associated only with female snails. This is the first sex-related allozyme reported for mollusks. No differences were detected in the electrophoretic mobilities of the 26 polypeptide chains separated in each of the three species by sodium dodecyl sulfate-polyacrylamide slab gel electrophoresis. The molecular weights of the polypeptide molecules ranged from 11,500 to 96,000.

The freshwater leech *Alboglossiphonia heteroclita* was found in 13.2% of the field-collected *Parafossarulus manchouricus* observed, and pleurolophocercous cercariae were found in 2.99% of the specimens. These parasites were not found in the other two snail species.

Laboratory-bred *Parafossarulus manchouricus* were susceptible to *Clonorchis sinensis*, with an overall infection rate of 15%. *Gabbia misella* and *Bithynia tentaculata* were refractory to infection with *C. sinensis*, and therefore do not need to be emphasized in snail surveys for clonorchiasis.

INTRODUCTION

The most medically important snail species of Korea is *Parafossarulus manchouricus* (Bourguignat), a member of the freshwater prosobranch family Bithyniidae. The parasite that this snail transmits to humans is *Clonorchis sinensis* (Cobbold), the "Chinese liver fluke". This trematode worm is one of the main snail-borne parasites of the Orient, where it infects hundreds of thousands of people in China, Japan, Korea, Vietnam and presumably parts of India. *P. manchouricus* is the main species, or perhaps the only species, of the generic group

Parafossarulus. The distribution of this snail, as far as is known, is the same as the trematode parasites it transmits. A second bithyniid species occurs in Korea, *Gabbia misella* Gredler. This species also has been suggested as an intermediate host of *C. sinensis* (Soh, 1978). Critical information on *P. manchouricus* and *G. misella*, as well as the whole family to which they belong, is very limited. There is no agreement on the number of species or genera in the family. Taxonomic opinions on the genera vary widely, and no one has made an attempt to catalogue or to evaluate the species. The dearth of information on these snails is undoubtedly partly responsible for the lack of control and eradication of clonorchiasis.

Clonorchiasis is the most serious and prevalent snail-borne disease in Korea. The disease occurs in nearly all provinces in South Korea, but it is especially prevalent in the southernmost provinces, where an estimated 20% of the people are infected. In spite of this, critical studies on Korean Bithyniidae are almost non-existent. Therefore, this study was initiated to investigate aspects of the biology (laboratory culture, spawning and growth, external morphology and radula, chromosomes, allozymes and parasites) of the Korean Bithyniidae, *Parafossarulus manchouricus* and *Gabbia misella*, and to compare Korean populations of these species with populations from other Far Eastern countries. Also, it was felt that a comparison of these two Korean species of Bithyniidae to *Bithynia tentaculata* (Linnaeus), the most widely distributed and nomenclaturally important species of the family, was especially pertinent.

Prior to the initiation of my studies, bithyniid snails had never been cultured in the laboratory. However, independent of my own successful culture of bithyniid snails, Kruatrachue et al. (1982) cultured several Thai species, but with somewhat different techniques than I used. Previous observations on external morphology of Bithyniidae are those of Abbott (1948) on *Gabbia misella* of Japan, and Baker (1928) and Taylor (1966) on North American *Bithynia tentaculata*. Chromosome numbers, all n=17, had been reported previously for four species of Bithyniidae, *B. tentaculata, B. leachi* (Sheppard), *B. usseriensis* Büttner & Ehrmann and *Mysorella costigera* (Küster), but no karyotype studies had ever been published. No information was available on isozymes or allozymes, or on parasites (other than *Clonorchis sinensis*) infesting Bithyniidae. Whether or not other bithyniid species were susceptible to infection with *C. sinensis* was not known.

The Bithyniidae are found sporadically throughout much of the world, including Eurasia, Africa and Australia. Their presence in the Western Hemisphere – in the North American Great Lakes-St. Lawrence region – generally is believed to be due to introductions by human agency, although Baker (1928) found evidence that bithyniids occurred in North America in Pleistocene times. By malacological standards, the family is not a large one, in that any one geographical region (except Thailand) usually has only one or few species.

The Bithyniidae often have been considered to be an independent family, but just as frequently they have been placed within the Hydrobiidae, usually as a subfamily. Arguments may still be forthcoming to follow the latter placement. However, Taylor (1966) has argued convincingly that the bithyniids should be separated from the hydrobiids and transferred to the Viviparoidea (Ampullarioidea), and this procedure has been followed most recently by Burch (1982) in his revision of the North American freshwater gastropods. Ampullarioid characters of bithyniids are their size (adult shells are more than 10 mm long), calcareous operculum with paucispiral nucleus and concentric edges, nuchal lobes of the head-foot, relatively long, flexible and acute tentacles, yellow and orange skin pigment granules, spirally constructed fecal pellets, use of the ctenidium in food gathering, pallial innervation of the penis, and dimorphic sperm (Taylor, 1966).

A review of the taxonomy of the family Bithyniidae on a world-wide basis is not within the scope of this study, but it might be mentioned that the two most recent compendia on gastropod classification, Thiele (1929) and Wenz (1938-44), list three and two genera, respectively, for the Bithyniidae. Thiele recognized as genera *Bithynia* (with four subgenera), *Pseudovivipara* Annandale [China] and *Mysorella* Annandale [India and Lake Tanganyika].

He included *Gabbia* Tryon as a subgenus of *Bithynia* and *Parafossarulus* Annandale as a section of the subgenus *Hydrobioides* Nevill. Wenz recognized only two genera: *Bulimus* [=*Bithynia*], with 12 Recent subgenera (including *Gabbia, Parafossarulus* and *Pseudovivipara*), and *Mysorella*. Of Wenz's subgenera of *Bithynia*, four are listed as having only one species, seven as having few species, and only *Gabbia* as having numerous species. The distribution of *Gabbia* is recorded as Australia, India, Sunda Island, Africa and southern Europe. *Mysorella* has only one or two species.

In Korea, three species of bithyniid snails have been recognized: *Parafossarulus manchouricus, Gabbia misella* and *G. kiusiuensis* (Hirase). However, the generic-group names to which the species have been assigned have differed and the taxonomic hierarchial rank of the various generic-group names have not always been the same (see Table 1). Also, the distinction between *G. misella* and *G. kiusiuensis* has been questioned, with the two names sometimes considered to be synonyms.

TABLE 1. Nomenclature used for Bithyniidae found in Korea.

Taxon name	References
*Parafossarulus manchouricus**	
Parafossarulus striatulus japonicus	Walker, 1927
Bithynia (subgenus *Hydrobioides* [section *Parafossarulus*])	Thiele, 1929
Bulimus [=*Bithynia*] (subgenus *Parafossarulus*)	Wenz, 1938-44
Parafossarulus manchouricus	Abbott, 1948; Kwon & Habe, 1979
Bithynia (subgenus *Parafossarulus*) *manchouricus*	Pace, 1973
*Gabbia misella**	
Bithynia (subgenus *Gabbia*)	Thiele, 1929
Bulimus [=*Bithynia*] (subgenus *Gabbia*)	Wenz, 1939
Bulimus [=*Bithynia*] *misellus*	Abbott, 1948
Bithynia kiusiuensis	Hirase & Taki, 1951; Habe, 1977
Bithynia (subgenus *Bithynia*) *misella*	Pace, 1973
Bulimus [=*Bithynia*] *kiusiuensis*	Soh, 1978
Gabbia misella	Kwon & Habe, 1979

**Parafossarulus manchouricus* and *Gabbia misella* are the taxon names used in the current paper for the Korean bithyniids.

MATERIALS AND METHODS

Sources of snails

Three species of snails were used in this study: *Parafossarulus manchouricus, Gabbia misella* and *Bithynia tentaculata*. Two of the species, *P. manchouricus* and *G. misella*, came from Korea. Other populations of *P. manchouricus* came from Japan and Taiwan. *B. tentaculata* came from the U.S.A., Germany and Portugal. All of the snails used in this study were initially field collected. The foreign snails were mailed to me in Ann Arbor. During their transit, they were kept wet. Additional details about the snails are given in Table 2. Voucher specimens have been deposited in the Museum of Zoology, The University of Michigan (UMMZ 250173-250176, 250254-250260).

TABLE 2. Populations of *Parafossarulus manchouricus*, *Gabbia misella* and *Bithynia tentaculata* collected from various countries.

Species	Localities collected (collector)	Date collected	Habitat
P. manchouricus			
Kimhae strain	Kimhae, Korea (J.K. Chang)	28-V-81	Ditch
Kunsan strain	Kunsan, Korea (J.K. Chang)	25-IX-81	Ditch
Kwangju strain	River Whangyong, Kwangju, Korea (J.K. Chang)	27-IX-81	River
Chongpyung strain	Chongpyung, Korea (J.K. Chang)	27-IX-81	Fish farm
Haman strain	Haman, Korea (J.K. Chang)	13-X-81	Ditch
Japan strain	Kurume, Japan (I. Miyazaki)	29-X-81	NR
Taiwan strain	Taipei, Taiwan (P. C. Fan)	18-XII-81	NR
G. misella	Gongju, Korea (H.D. Kim)	9-IX-81	Pond
B. tentaculata			
Michigan strain	Hamlin Lake, Ludington, Michigan, U.S.A. (P.R. Chung)	18-VIII-81	Lake
Germany strain	Bodensee, Tübingen, Germany (C. Meier-Brook)	15-IX-81	Lake
Portugal strain	Portugal (M.A. Grácio)*	7-VII-81	NR

*The Portugal strain of *B. tentaculata* was propagated in the laboratory from a single female snail.

NR = not recorded.

Culture methods

Snails

Two local strains (Kimhae and Kunsan, Korea) of *Parafossarulus manchouricus*, one local strain (Gongju, Korea) of *Gabbia misella*, and two geographical strains (German and Portuguese) of *Bithynia tentaculata* were mainly used in the culturing studies, although other strains of bithyniids also were raised in the laboratory.

Containers

After receipt, the snails were maintained in conventional aquaria. These were glass aquaria (20 x 25 x 35 cm) which held seven liters of water. A general view of the arrangement of the snail aquaria on the shelving unit is shown in Fig. 1. Stock cultures of extra snails were kept in larger tanks (Fig. 2). Glass finger bowls and small plastic trays containing about 350 ml of water were used for the cultivation of egg masses and newly hatched snails. Commercial plastic trays (7.5 x 20 x 30 cm) designed for plant seedlings sometimes were employed as aquaria, especially for the cultivation of medium-sized growing snails, since the trays were easy to handle and reasonable in price. Each tray can contain 1,500 ml of water.

Environmental parameters

Water. Initially, tap water was conditioned before use simply by adding 4-5 drops of 5% sodium thiosulfate solution to each aquarium for dechlorination. However, later the pH value of water coming from Ann Arbor water faucets was raised to 9.5, which is enough to kill aquatic organisms, including the snails. Thereafter, tap water was contained in a 7-gal (26.6 l) plastic jar, to which was added 1 ml of 1 N HCl solution and 5% sodium thiosulfate solution per gallon (per 3.8 l). This water was aerated for one week prior to use. Following this treatment, the pH of the conditioned water was 6.5-7.0.

Light. The aquaria were placed on shelves in a shelving unit and exposed alternately to 12 hrs of artificial light (provided by a 15-watt cool, white fluorescent tube) and 12 hrs of darkness. An automatic timer

FIG. 1. General view of a shelving unit. The glass aquaria and the large and small plastic trays are beneath a cool, white 15-watt fluorescent light. A rubber tube runs to each container to provide aeration.

FIG. 2. Stock cultures of bithyniid snails in larger aquaria.

controlled the cycling of the light.

Aeration. The water of all the glass aquaria, the finger bowls and the plastic trays for the baby snails was continuously aerated by bubbling air from a centrally located air compressor through the water. The aerators in the glass aquaria consisted of a plastic container containing grains of charcoal covered with limestone and topped with cotton or glasswool.

Temperature. The temperature of the aquarium room was maintained by air-conditioning units during the summer and by thermostatically controlled central heating during the winter. The temperature in the laboratory room in which some containers were maintained was controlled by a thermostat in the winter, but was not air-conditioned in the summer. The water temperature for the aquaria ranged from 25-27°C.

Food. Three kinds of food were used for snails reared and maintained in the laboratory: natural periphyton, powdered green leaves (commercial Ceralife®) and commercially prepared fish-food flakes (Tetra SML®, Tetra Co., D-452 Melle, West Germany). Tetra SML flakes were supplied to the adult snails twice a week. Daily supply of food was avoided because an excess of food in the water caused a fungus bloom on the bottom of the aquarium, which made conditions in the containers unfavorable. Ingredients of Tetra SML are fish meal, oat gruel, roe, shrimp meat, salmon eggs, fish-liver meal, squid, plankton, cyclops, agar agar, wheat-germ oil, cod-liver oil, carotene and fish-bone lime. Composition (as dry matter) of Tetra SML includes crude protein (46%), crude fat (5%) and crude fiber (8%).

Ceralife together with periphyton was used in rearing young snails until they became adults. The Ceralife powder was used by the snails to make food "sausages" prior to ingestion.

Small stones covered with natural periphyton were collected from Fleming Creek in the vicinity of The University of Michigan's Botanical Gardens. The slimy mucilage film discharged by diatoms on the stones was a good natural food source, especially for growing baby snails. Permanent slides of diatoms were prepared for taxonomic identification. The diatoms included mainly *Navicula* spp. and *Gomphonema* spp., and other as yet unidentified taxa. The stones were placed in the finger bowls, in the plastic trays and glass aquaria. The stones were replaced every two weeks.

Aquarium environment. The periphyton-covered stones served not only as food but also as substrate for the snails. No mud was added as a substrate. Long established aquaria usually became filled with filamentous green algae (mainly *Rhizoclonium hieroglyphicum* (Kützing), but also *Oedogonium* sp., *Ulothrix* sp. and *Closterium* sp.). These algae originated from the field-collected snail shells as well as from the stones. Sometimes aquatic plants, such as *Elodea*, *Myriophyllum* and *Sagittaria*, were placed in the aquaria in order to stabilize the aquarium environment. No definite relationships between the presence of particular plants and the survivorship of snails were observed in the present study. However, death of snails in aquaria with dense filamentous green algae was occasionally observed.

Snail maintenance

The number of snails per tank did not exceed 20 for the larger snails (7-10 mm shell length) or 50 for the 3-7 mm shell size class. As many as several hundred newly hatched snails were maintained in each 7-liter aquarium.

After the snails had laid eggs in the aquaria, egg masses were scraped from the aquaria walls with a razor blade and placed into 350-ml glass finger bowls or small plastic trays with conditioned water. The water in the containers was supplied with continuous aeration until the baby snails hatched. The egg masses were maintained under constant fluorescent illumination at temperatures between 25° and 27°C. The eggs of *Parafossarulus manchouricus* and *Bithynia tentaculata* hatched approximately two weeks after being laid and the eggs of *Gabbia misella* in about three weeks (see Table 5). The newly hatched snails were then transferred with a Pasteur pipette to plastic culturing trays. The young were fed on powdered Ceralife (powdered green leaves) and periphyton. During cultivation of the young snails, the lengths and widths of their shells were measured every three days with an ocular micrometer in a dissecting microscope.

Egg-laying characteristics

Egg mass data were obtained by observing five laboratory populations: two strains of *Parafossarulus manchouricus, Gabbia misella* and two strains of *Bithynia tentaculata*. In each of the tanks of *P. manchouricus* (Kimhae and Kunsan strains) and *G. misella*, there were 20 snails: 10 females and 10 males. In the German strain of *B. tentaculata*, there were 15 snails: 10 females and 5 males. In the Portuguese strain of *B. tentaculata*, there was only one snail, a female. The egg masses were counted every third day.

For *Parafossarulus manchouricus* (Kunsan strain), *Gabbia misella* and *Bithynia tentaculata* (Michigan strain), egg masses were compared as to number of eggs per egg mass, size of eggs and incubation period. For the latter, the egg masses were transferred to finger bowls and observed every day.

Morphological studies

Morphological studies included shells, opercula, mantle pigmentation, radulae and egg masses. Observations were made on shell shape, size ratios of various parts, characteristics of whorls, sutures, peritreme,

columella and surface sculpture (including microsculpture). These characteristics were observed with the use of a stereoscopic microscope, in some cases with a compound light microscope and with a scanning electron microscope [SEM]. All drawings were made with the aid of a Wild M5 stereoscopic microscope equipped with a drawing tube.

In order to gather additional information on the external morphologies of the bithyniid snails used in this study, the shell and aperture lengths of the snails were measured with a dial caliper and expressed in terms of the relative spire height (H_{sp}), which is the ratio of the shell length (l_{sh}) over aperture length (l_a) of the adult shells (Vermeij, 1973). Morphological differences (H_{sp} values) between pairs of populations were tested for statistical significance by use of the Student's *t* test.

Measures of the intensity of external shell sculpture were expressed by assigning integral consecutive ranks, starting with Rank 1 as the smoothest specimen in the series being compared (Vermeij, 1973) (see Table 9).

The radulae were prepared for scanning electron microscopy by macerating fresh buccal masses in a 10% potassium hydroxide solution for 24 hrs at room temperature and then removing the radulae from the disintegrating muscle tissues and adherent membranes of the buccal mass. Each separated radula was placed in a vial containing 70% ethanol and cleansed in an ultrasonic cleaner for 5-15 sec, and then secured with double sticky tape on an SEM stub (a drop of double distilled water was first placed on the tape on the stub, and the radula was transferred to the tape with a pipette; the radula was spread out with the aid of a dissecting microscope, microforceps and fine brush; when the radula was in the proper position on the stub, excess water was removed with a brush or capillary tube). The completely dried radulae were stored in a dust-free container until the gold coating was applied. The gold-coated radulae were observed with a JEOL JSM-U3 scanning electron microscope.

A juvenile shell and operculum were selected for SEM study with the same procedure as used for the radulae. A juvenile was used because its sculpture would be less affected than older snails by abrasion and erosion.

Chromosome cytology

The snail specimens used in this study were *Parafossarulus manchouricus* (Haman strain), *Gabbia misella* and *Bithynia tentaculata* (Michigan and Germany strains). Chromosomes were observed in both male and female snails: 10 males and five females of the Michigan strain of *B. tentaculata*, three males and three females of the German *B. tentaculata*, 14 males and 10 females of the Haman *P. manchouricus* and six males and five females of *G. misella*. Since cell divisions occur more frequently in reproductive tissue, and meiosis occurs there as well, the organs used for chromosome studies were the gonads. The cytological preparations included treatment with a spindle inhibitor, tissue fixation and acetic-orcein squash procedures for temporary and permanent mounts. The methods followed were those of Patterson & Burch (1978), with some minor modifications.

The shell of each snail was gently crushed with a scalpel or with a laboratory rubber hose clamp so as not to damage the vital organs, and the pieces of shell were removed with forceps. Ten to 15 animals were then pooled together in a square watch glass, a small Petri dish or a small glass vial containing an adequate amount of conditioned water. The conditioned water was soon removed with a syringe or a Pasteur pipette, and the residue removed by absorbent paper. Fifteen ml of 0.00025% Velban® (vinblastine sulfate, Eli Lilly and Co., Indianapolis, Indiana, U.S.A.) in an isotonic solution of 0.04% NaCl was added to the container. Velban is a spindle inhibitor; the solution to which the snails were exposed was prepared from a stock solution of 1 mg/ml of vinblastine sulfate dissolved in bacteriostatic sodium chloride injection solution. The snails were left in this solution for 3 hrs at room temperature. Then, half the total volume of the solution was withdrawn using a syringe and replaced with the same amount of 0.02% NaCl solution. The snails were kept in this solution for 30 min before it was withdrawn. The entire fluid was completely withdrawn again, and 15 ml of ¼ dilution of 0.00025% Velban (0.0000675%) in 0.02% NaCl solution was added. The snails were kept in this hypotonic solution for 30 min at room temperature. The hypotonic solution helped to keep the chromosomes loose and facilitated their spread and separation when the squash procedure was performed. All the crushed snails treated with the spindle inhibitor were alive and in apparent good condition before being fixed. The snails were fixed by withdrawing the hypotonic solution from the snail containers and immediately replacing it with Carnoy's fixative (glacial acetic acid, chloroform and 95% ethanol, 1:3:6 parts by volume) or modified Carnoy's fixative (glacial acetic acid and 95% ethanol, 1:3 parts by volume). Female snails were treated with Carnoy's fixative first for 15 min and then with modified Carnoy's fixative. This procedure was performed in order to get rid of lipids in the ovary by the chloroform in the Carnoy's fluid. The amount of fixative solution was at least 10 times greater in volume than the tissue. Although the fixing time varied according to the size and the condition of the tissue, the snail gonads usually were stained approximately an hour after fixation. The fixative in which the snails were to be stored for future use was changed after 24 hrs and kept in the refrigerator at 2-10°C.

Chromosome preparations were made using the acetic-orcein squash technique. Observations were made with Nikon (Nippon Kogaku) compound microscopes using 100x (n.a. 1.25) oil immersion objectives

and 10x and 30x oculars. The chromosomes were drawn with the aid of a camera lucida and reproduced at a table top magnification of about 5,000x. Photographs were taken using a 10x ocular, oil immersion objective, a Kodak 57A green filter and Kodak Technical Pan Film.

Karyotypes of the chromosomes were prepared from camera lucida drawings and photographs. The camera lucida drawings were especially helpful in determining the exact position of centromeres of the mitotic metaphase chromosomes and in matching the pairs of homologues. A dial caliper was used in measuring on the drawing paper the chromosome arm lengths and total chromosome lengths. The chromosomes were divided into three groups according to the position of their centromeres. Chromosomes whose short arm was less than 1/20th of the total chromosome length [TCL] (or with an arm ratio >19) were called "acrocentric" chromosomes; chromosomes with an arm ratio between 19 and 2 were called "submetacentric"; and chromosomes with an arm ratio between 2 and 1 were referred to as "metacentrics" (White, 1973). Chromosome lengths were standardized as a percentage of the total haploid complement length (% TCL) (Paris Conference, 1971). The chromosomes in each karyotype were arranged in descending order by size and according to the positions of their centromeres.

Allozyme electrophoresis

Horizontal starch gel electrophoresis

Snail populations employed. The snail populations utilized in this study were field collected from the following allopatric localities in order to compare genetic variation: Haman and Chongpyung, Korea (*Parafossarulus manchouricus*); Kurume, Japan (*P. manchouricus*); Taipei, Taiwan (*P. manchouricus*); Michigan, U.S.A. (*Bithynia tentaculata*); Bodensee (Lake Constance), Germany (*B. tentaculata*); southern Portugal (*B. tentaculata*); and Gongju, Korea (*Gabbia misella*). Prior to the electrophoretic analyses, the snails of each population were placed in plastic trays and starved for 48 hrs to clear their digestive tracts. All of the snails also were checked for the shedding of trematode cercariae. Only parasite-free snails were employed in this study. The snails in each population were separated into male and female groups and then frozen and stored at -90°C.

Sample preparation. Individual animals were thawed and then crudely minced with a scalpel on ice. The resulting slurry of each individual animal was placed into 1 ml Sorvall® centrifuge tubes with 200 µl of distilled water and sonicated for a few seconds with a Bronwill Biosonic® III sonicator equipped with a microprobe tip. Following sonication, the samples were centrifuged at 4°C in a Sorvall RC-2B refrigerated centrifuge (equipped with a SS-34 rotor) at 5,500 rpm for 30 min, after which the resulting clear supernatant was collected in 50 µl aliquots in plastic microcentrifuge tubes and stored at -70°C until used for horizontal starch gel electrophoresis. The total wet weights of animals without their shells were approximately 0.08 gm for *Parafossarulus manchouricus* and *Bithynia tentaculata*, and 0.03 gm for *Gabbia misella*. The average protein concentrations in 200 µl of tissue extracts of *P. manchouricus*, *B. tentaculata* and *G. misella* were 357 µg/ml, 372 µg/ml and 189 µg/ml, respectively. A standard curve for the estimation of these proteins by the Lowry et al. (1951) method was constructed using bovine serum albumin (Sigma Chemical Co., St. Louis, Missouri, U.S.A.) as a standard protein.

Starch gel electrophoresis. A 15% starch gel was prepared using equal amounts (22.5 gm) of Electrostarch (Lot No. 392) and Connaught Starch Hydrolysed (Lot No. 168-1) in 300 ml of gel buffer. The starch was mixed with the gel buffer in a side-arm filter flask and heated over a Bunsen burner with a medium hot flame as described by Smith (1968) and Brewer (1970). The cooked starch gel solution was then degassed for one minute with a water aspirator, poured into a plexiglass frame (14 x 14 x 1 cm) on a 0.63 cm thick plate-glass bottom and covered with a glass plate which had been warmed on the hot plate. Special care was taken to get rid of air bubbles in the starch gel when covering the glass plate on the gel mold. After cooling for 1 hr at room temperature (23-25°C), the gel was kept overnight in a refrigerator (2-4°C).

The samples to be electrophoresed were applied to 9 x 5 mm pieces of Whatman 3 MM chromatography paper and inserted into a slot cut 3 cm from the cathodal end of the gel. Usually 18 to 20 samples were inserted per slab.

The gel thus loaded was placed horizontally over two buffer trays with platinum electrodes. Paper wicks (Handywipe® tissue papers or Bolt® paper towelling) were used to establish contact between the gel and the electrode buffer in the trays. The top of the gels was covered with plastic film (Handiwrap®) to prevent moisture loss during operation. The entire gel assembly was placed into a refrigerator at 2-4°C and connected to a constant voltage power supply (Heathkit model PS-4, IP-32 or IP-17).

Following electrophoresis, the gels were sliced horizontally into five 2 mm thick slices using a Buchler-type gel slicer. Each sliced gel was then transferred singly into a staining dish for a specific enzymatic activity stain. Incubation was done in complete darkness to avoid any undesirable effects of light on the stain. The enzymatic activities usually appeared within about 20 min in an incubator. The stained gel was fixed by simply discarding the staining solution and rinsing once with tap water and adding 10% acid alcohol fixative (5 parts of 95% ethanol or methanol, 4 parts of water and 1 part of glacial acetic acid by

volume). The fixative was replaced with tap water 1 hr after fixation and the gels then kept moist in plastic bags in the refrigerator.

Starch gel electrophoresis buffers. Four different buffer systems were routinely used to detect various enzymatic activities (Table 3). Buffer system I was the discontinuous buffer system of Poulik (1957). The gel buffer contained 76 mM Tris and 5 mM citric acid. The electrode buffer of system I contained 0.3 M boric acid and 60 mM NaOH. Buffer system II was the discontinuous Tris-citrate/lithium hydroxide-borate system of Ashton & Braden (1961). The gel buffer contained 90% of a solution containing 0.05 M Tris and 0.008 M citric acid and 10% of electrode buffer. The electrode buffer contained 0.19 M boric acid and 0.03 M LiOH. Buffer system III was the Tris-EDTA-maleate buffer system at pH 7.4 (Spencer et al., 1964). The electrode buffer contained 0.1 M Tris, 0.1 M maleic acid, 10 mM EDTA [ethylene diamine tetraacetic acid (disodium salt)] and 10 mM $MgCl_2$. The pH was adjusted to 7.4 using 1 N NaOH

TABLE 3. Starch gel buffer systems employed for the detection of various enzyme activities in *Parafossarulus manchouricus*, *Bithynia tentaculata* and *Gabbia misella*.

E.C. No.*	Enzyme	Buffer system†			
		I	II	III	IV
1.1.1.8	α-glycerophosphate dehydrogenase	+	+	ND	–
1.1.1.14	Sorbitol dehydrogenase	+	±	–	ND
1.1.1.30	β-hydroxybutyrate dehydrogenase	+	–	–	–
1.1.1.37	Malate dehydrogenase	±	±	ND	ND
1.1.1.43	6-phosphogluconate dehydrogenase	ND	ND	±	ND
1.2.3.2	Xanthine oxidase	+	–	ND	ND
1.4.3.3	D-amino acid oxidase	–	–	ND	ND
2.6.1.1	Glutamate-oxaloacetate transaminase	+++	++	++	ND
3.1.1.1	Esterase				
	in α-naphthyl acetate	+++	++	+	ND
	in α-naphthyl butyrate	++	+	ND	ND
	in α-naphthyl propionate	+	++	ND	ND
3.1.3.1	Alkaline phosphatase	+++	+	–	+++
3.1.3.2	Acid phosphatase	++	+++	++	++
3.4.11 or 3.4.13	Peptidase				
	Alanine aminopeptidase	+++	+++	ND	ND
	Leucine aminopeptidase	++	+++	+	+

*E.C. No. = Enzyme Commission number.

†I = The discontinuous buffer system of Poulik (1957); II = the discontinuous Tris-citrate/lithium hydroxide-borate system of Ashton & Braden (1961); III = the Tris-EDTA-maleate buffer system at pH 7.4 (Spencer et al., 1964); IV = the continuous Tris-EDTA-borate buffer system at pH 8.6.

Abbreviations: +++ = excellent results; ++ = good results; + = satisfactory results; ± = non-satisfactory results with poor resolution; – = no reaction at all; ND = not done.

solution. The gel buffer was a 10-fold dilution of the electrode buffer. Buffer system IV was a continuous Tris-EDTA-borate system at pH 8.6. The gel and electrode buffers were prepared by dilution from a stock solution containing 0.9 M Tris, 0.5 M boric acid and 0.1 M EDTA (disodium salt). The gel buffer contained 40 ml of stock solution diluted to 1 l. The electrode buffer contained 450 ml of stock solution diluted to 4 l with distilled water.

Electrophoresis was terminated after the bromphenol blue marker dye (0.1% in distilled water) had migrated 9 cm from the origin. It took about 6 hrs at 25 mA/gel for buffer systems I and II, 8 hrs at 45 mA/gel for buffer system IV and 18 hrs at 30 mA/gel for buffer system III. The buffer systems used most routinely were I and II. The enzyme systems and the buffer systems in which they were resolved are listed in Table 3.

Enzyme assays. Thirteen enzymes for the eight populations of bithyniid snails were tested in this study. The assay solutions used for detecting these enzymes followed Coles (1969a,b), Shaw & Prasad (1970), Selander et al. (1971) and Kitikoon (1982b). The compositions of assaying solutions follow.

α-glycerophosphate dehydrogenase [α-GPDH] (buffer system I or II): α-D,L-glycerophosphate (100 mg, 0.1 M $MgCl_2$ (1 ml), β-nicotinamide dinucleotide (NAD) (20 mg), 3-(4,5-dimethyl thiazolyl-2)-2,5-diphenyl tetrazolium bromide (MTT) (15 mg), phenazine methosulfate (PMS) (4 mg), 0.2 M Tris [Tris-hydroxymethyl-aminomethane; 2-amino-2-hydroxymethyl-1; 3-propanediol]-HCl buffer, pH 8.0, to make 50 ml. MTT was the only tetrazolium salt used. It is considerably less expensive than NBT [nitroblue tetrazolium] and is essentially equivalent. MTT, NAD and PMS were dissolved in distilled water with known concentration and kept in a freezer until used.

Sorbitol dehydrogenase [SoDH] (buffer system I): sorbitol (250 mg), NAD (15 mg), MTT (15 mg), PMS (3 mg), 0.2 M Tris-HCl buffer, pH 8.0, to make 50 ml.

β-hydroxybutyrate dehydrogenase [β-HBDH] (buffer system I): β-hydroxybutyric acid (40 mg), NAD (10 mg), MTT (20 mg), PMS (5 mg), 0.2 M Tris-HCl buffer, pH 8.0, to make 50 ml.

Malate dehydrogenase [MDH] (buffer system I or II): 1.0 M L-malate, pH 7.0 (5.0 ml), NAD (10 mg), MTT (20 mg), PMS (5 mg), 0.2 M Tris-HCl buffer, pH 8.0, to make 50 ml.

6-phosphogluconate dehydrogenase [6-PGDH] (buffer system III): 6-phosphogluconic acid (25 mg), 0.1 M $MgCl_2$ (10 ml), MTT (20 mg), PMS (5 mg), NAD (10 mg), 0.2 M Tris-HCl buffer, pH 8.0, to make 50 ml.

Xanthine oxidase [XO] (buffer system I): hypoxanthine (80 mg), MTT (10 mg), PMS (5 mg), 0.2 M Tris-HCl buffer, pH 7.5, to make 50 ml. The hypoxanthine was first dissolved in 1-2 ml of 1 N NaOH, to which was added the 0.2 M Tris-HCl buffer, pH 7.5. The final pH of this solution was approximately 8.0.

D-amino acid oxidase [AAO] (buffer system I or II): D,L-alanine (400 mg), MTT (10 mg), PMS (3 mg), 0.2 M Tris-HCl buffer, pH 8.0, to make 50 ml.

Glutamate oxaloacetate transaminase [GOT] (buffer system I, II or III): α-keto glutarate (100 mg), α-aspartic acid (150 mg), pyridoxal-5-phosphate (5 mg), fast blue BB salt (100 mg), 0.2 M Tris-HCl buffer, pH 8.0, to make 50 ml.

Esterase [EST] (buffer system I, II or III): 1% substrate (w:v) in acetone (1 ml), fast blue RR salt (35 mg), 0.2 M Tris-HCl buffer, pH 7.4, to make 50 ml; *substrates* – α-naphthyl acetate, α-naphthyl butyrate and α-naphthyl propionate.

Alkaline phosphatase [AlP] (buffer system I, II or IV): β-naphthyl acid phosphate (50 mg), 0.1 M $MgCl_2$ (2 ml), fast blue RR salt (50 mg), 0.2 M Tris-HCl buffer, pH 9.0-9.5 to make 50 ml. The gel slice was incubated in the stain buffer for 1 hr prior to the incubation for enzymatic reactions.

Acid phosphatase [AcP] (buffer system I, II, III or IV): α-naphthyl acid phosphate (50 mg), fast black K salt (50 mg), 0.2 M acetate buffer, pH 5.0, to make 50 ml. The gel slice was incubated in the pH 5.0 acetate buffer for 1 hr prior to the incubation for enzymatic reactions.

Alanine aminopeptidase [AAP] (buffer system I or II): *solution 1* – D,L-alanyl-β-naphthylamide HCl (20 mg), 0.1 M $MgCl_2$ (1 ml), 0.1 M phosphate buffer, pH 7.0, to make 50 ml; *solution 2* – fast black K salt (30 mg), 0.1 M phosphate buffer, pH 7.0, to make 50 ml. The gel slice was incubated in solution 1 for 30 min, then the solution was decanted and solution 2 added. D,L-alanyl-β-naphthylamide HCl was first dissolved in 0.5 to 1.0 ml of N,N-dimethyl formamide [DMF] and then mixed with the buffer. Extreme care was taken in handling D,L-alanyl-β-naphthylamide HCl, a carcinogen.

Leucine aminopeptidase [LAP] (buffer system I, II, III or IV): *solution 1* – L-leucyl-β-naphthylamide HCl (20 mg), 0.1 M $MgCl_2$ (1 ml), 0.1 M phosphate buffer, pH 7.0, to make 50 ml; *solution 2* – fast black K (50 mg), 0.1 M phosphate buffer, pH 7.0, to make 50 ml. The gel slice was incubated in solution 1 for 30 min, and then placed in solution 2. L-leucyl-β-naphthyl-amide HCl, a carcinogen, has to be dissolved in 0.5-1.0 ml of DMF first.

Sodium dodecyl sulfate-polyacrylamide slab gel electrophoresis [SDS-PAGE]

SDS-PAGE was carried out to determine if differences in protein structures could be detected among the bithyniid species. SDS-PAGE, using a "Protean Double Slab Electrophoresis Cell" (Bio-Rad Laboratories, Richmond, California, U.S.A.) apparatus, also can be used to determine the molecular weights of

polypeptide chains in oligomeric proteins. Individual snails were homogenized in a mortar with 2 M dimethyl formamide [DMF] in a 20% sucrose solution, and a small teaspoonful of fine sand was added to help grinding. After grinding for about 5 min, the specimens were centrifuged at 10,000 g for 10 min at 4°C, and the supernatants were discarded. The sediments were mixed with 1 ml of 0.01 M sodium phosphate buffer, pH 7.0, and centrifuged again at 10,000 g for 15 min at 4°C. After discarding the supernatants, 1 ml of 0.01 M sodium phosphate buffer, pH 7.0, containing 1% SDS, 1% β-mercapto-ethanol, 6 M urea and 0.02% bromphenol blue (sample buffer) was added and mixed well. The specimens were then boiled for 5 min to break the polypeptide chains to be detected on the gels. After boiling, the specimens were centrifuged at 27,000 g for 10 min at 4°C, and the supernatants (protein solution) were used for SDS-PAGE.

The gel buffer contained 7.8 gm of $NaH_2PO_4 \cdot H_2O$, 38.6 gm of $Na_2HPO_4 \cdot 7H_2O$, and 2 gm of SDS per liter. For the 10% acrylamide solution, 22.2 gm of acrylamide and 0.6 gm of methylenebisacrylamide were dissolved in water to give 100 ml of solution. Insoluble material was removed by filtration through Whatman No. 1 filter paper. The stock solution was kept at 4°C in a dark bottle. For the 10% acrylamide working solution, 15 ml of gel buffer were mixed with 13.5 ml of acrylamide stock solution. After deaeration, 1.5 ml of freshly made ammonium persulfate solution (15 mg per ml) and 0.045 ml of N,N,N′,N′-tetramethylethylenediamine [TEMED] were added for polymerization of the acrylamide. After mixing, the gel plates were filled with the acrylamide solution. The upper gel was made with 3% acrylamide solution. Then, 50 μl of the protein sample was loaded to each column of the gel, using a tuberculin syringe connected to plastic tubing. Electrophoresis was performed at a constant current of 8 mA per gel for 4 hrs at room temperature. The power was supplied by a "1420 B Constant Power Supply", and the gel buffer was used as the electrode buffer.

After electrophoresis, the gels were removed and placed in a pan containing 0.02% Coomassie Brilliant Blue R in 25% isopropanol and 10% acetic acid solution, and kept at room temperature overnight. The gels were removed from the staining solution, rinsed with distilled water and placed in a destaining solution containing 10% acetic acid and 25% isopropanol for a minimum of 2 hrs.

The bromphenol blue dye fronts of the gels after destaining and the positions of the blue protein zones were measured using a dial caliper and then stored in 7.5% acetic acid solution. The mobilities of the protein bands were calculated as mobility = $\frac{\text{distance of protein migration}}{\text{distance of marker dye migration.}}$

The mobilities of the standard marker proteins (0.16 for bovine serum albumin, 0.29 for ovalbumin, 0.72 for myoglobin and 0.79 for hemoglobin) were plotted against known molecular weights of these proteins (68,000 for bovine serum albumin, 43,000 for ovalbumen, 17,200 for myoglobin and 15,500 for hemoglobin) expressed on a semilogarithmic scale and a standard curve was constructed (Fig. 3). The migration distances of these standard proteins were 17.22, 30.83, 74.43 and 82.48 mm, respectively (the distance of the marker dye migration was 104 mm).

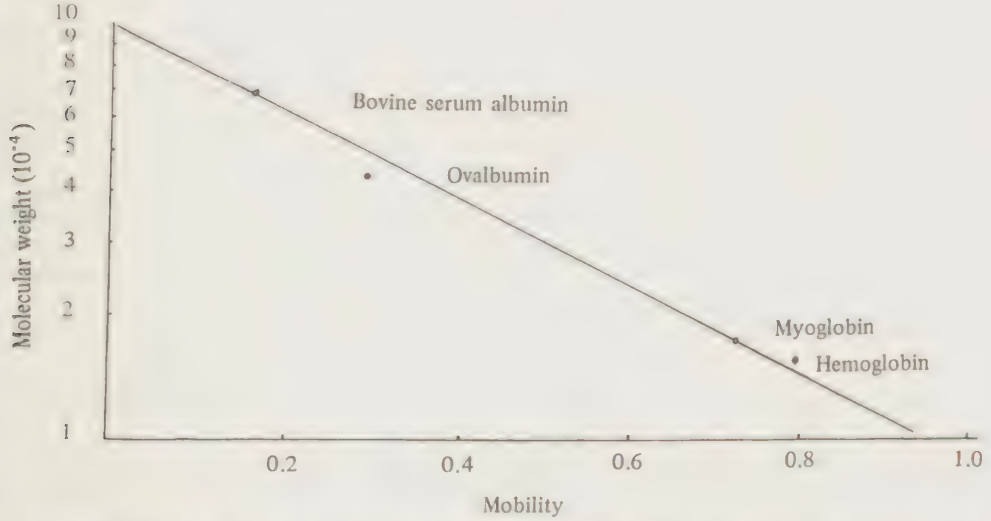


FIG. 3. A standard curve of the electrophoretic mobilities of the four marker proteins used for the determination of molecular weights of polypeptide chains (r = -0.97).

Parasitology

Natural infections

Field-collected specimens of five populations of *Parafossarulus manchouricus* (Haman, Kunsan, Kwangju, Chongpyung and Kimhae in Korea) and one local population of *Gabbia misella* (Gongju, Korea) were checked for natural infections of worm parasites. After collection, the snails were tightly packed in plastic boxes with wet surgical gauze or paper towels and shipped by air mail from Korea to Ann Arbor. The packages were about one week enroute. On arrival, the snails were introduced into temporary aquaria filled with conditioned water. Approximately 90% of the snails survived the trip.

The shells were carefully crushed using a screw-type aquarium hose clamp or a scalpel handle and, after removing broken pieces of shell, the exposed animals were examined. Under a dissecting microscope, the mantle of each animal was carefully teased to check for leeches.

The leeches were narcotized in 15% ethanol over a 30 min period. When the leeches no longer responded to pinching with a forceps, they were then rapidly drawn between the fingers and washed so that the secreted mucus was washed off. Next, the leeches were straightened and placed between two glass plates with gentle pressure. This preparation was then immersed in 20% formaldehyde to fix the leeches in this position. After the fluid had thoroughly penetrated and the leeches were stiffened, they were placed in vials containing 80% ethanol (Klemm, 1972b).

Annelid worms besides the leeches sometimes were found associated with the bithyniid egg masses. These worms were collected, preserved in 70% ethanol, transferred onto slide glasses for mounting with Lactophenol®, and the slides and coverslips sealed with nail polish for later morphological identification.

For the determination of trematode cercariae from the snails, each animal was placed in a glass vial (15 x 17 mm) containing 2 ml of aerated tap water, kept under a fluorescent light for several hours and the vial examined for the presence of shed cercariae. Later, the snails were crushed for further inspection for cercariae. In order to examine the ventral side of the cercariae, a drop of the solution containing the cercariae was placed on a cover slip. A slide glass was placed very slowly over the loaded cover slip until the two made contact. The glass slide then was turned right side up and the excess mounting fluid between the cover slip and the glass slide blotted by a strip of filter paper at the end of a cover slip. This preparation was sealed with vaseline around the cover slip to prevent evaporation of the mounting fluid for the duration of observation.

Susceptibility to infection with *Clonorchis sinensis*

Five dead cyprinid fish (*Pseudorasbora parva*) harboring *Clonorchis* metacercariae were mailed from Seoul, Korea, to Ann Arbor. After removing the visceral organs, the whole fish was minced and digested in artificial gastric juice at 37°C for several hours. The artificial gastric juice was composed of 3 gm of pepsin and 7 ml of concentrated HCl in 1 liter of distilled water. After incubation, the digested material in the gastric juice was poured into a strainer to get rid of the large pieces of tissue. The fine tissue suspension was washed several times with 0.85% NaCl solution. The number of *Clonorchis* metacercariae per known volume was counted under the low power (x100) of a light microscope.

Three adult rats were used for metacercarial infection. Each rat was infected orally with about 30 metacercariae, using a tuberculin syringe connected with a plastic tube. The infected rats were used as the source of eggs for the snail susceptibility studies. The wet stool pellets containing the *Clonorchis* eggs were collected from the pre-cleaned cages of the infected rats and emulsified with 0.85% NaCl solution. The emulsion was poured into a column of sieves (U.S.A. Standard Testing Sieves, nos. 40, 100, 200 and 325, W.S. Tyler, Inc., Mentor, Ohio, U.S.A.) arranged in descending order of mesh openings (425 μm, 150 μm, 75 μm and 45 μm, respectively). The final fine filtrates were collected in a large beaker (2,000 ml) and washed three times in conditioned water at 1,500 rpm for 5 min at 4°C to get rid of the NaCl. The final volume of the suspension containing the *Clonorchis* eggs was regulated to 50 ml, and then 0.02 ml of the suspension was pipetted with an automatic micropipette onto individual glass slides for counting the eggs.

For the susceptibility study, laboratory-bred *Parafossarulus manchouricus* and *Bithynia tentaculata* and field-collected *Gabbia misella* were maintained according to the culture methods described previously. All the snails were individually exposed to the *Clonorchis* eggs. Individual exposure was carried out by placing a single snail in a glass vial (15 x 17 mm) containing 12 *Clonorchis* eggs (in 0.02 ml of egg suspension) and 10 ml of conditioned water. The snails were starved for one day prior to exposure to the parasite eggs in order to increase the snails' appetite. The snails were left overnight (about 17 hrs) in the vials with the *Clonorchis* eggs. During this time they were kept under ceiling illumination (fluorescent lights) at room temperature (25-27°C). Twenty snails each of *P. manchouricus* and *B. tentaculata* and 15 snails of *G. misella* were exposed to the eggs and returned to their aquaria after exposure. After centrifugation, the eggs remaining in the vials were counted under the light microscope (x250) in order to know how many eggs had been ingested by the snails.

The snails were individually examined for the presence of *Clonorchis sinensis* cercariae, beginning at

the fifth week after exposure. Each snail was placed in a glass vial containing 3 ml of conditioned water, kept under the ceiling fluorescent light for 5 hrs, and the vial examined under the dissecting microscope for the presence of cercariae. All the snails were checked weekly until the 12th week after exposure, but no snail was crushed to see the developing sporocysts [the snails were needed for other studies].

RESULTS

Culture of bithyniid snails

Laboratory culture of bithyniid snails has been considered to be extremely difficult, if not impossible. However, in my research, the various bithyniid species studied were cultured and maintained very successfully with the care they received, so more elaborate experiments were not performed. Egg-laying characteristics and snail growth are discussed in the following sections.

Egg-laying characteristics and snail growth (Fig. 4)

The adult snails of the Kimhae strain of *Parafossarulus manchouricus* were received by air mail in May 1981 and immediately put into aquaria. The snails first laid egg masses on the seventh day after the onset of rearing and then laid eggs continuously until June 1981. The snails then stopped laying eggs for nine months and started laying again in March 1982 (Table 4). Culture of the Kunsan strain of *P. manchouricus* was initiated in September 1981.

TABLE 4. Number of egg masses laid in the laboratory by field-collected *Parafossarulus manchouricus*, *Gabbia misella* and *Bithynia tentaculata*.

Year	Month	*P. manchouricus**		*G. misella**	*B. tentaculata*	
		Kimhae	Kunsan	Gongju	Germany†	Portugal‡
1981	May	15				
	June	23				
	July	–				–
	Aug.	–				2‡
	Sep.	–	–	–	–	–
	Oct.	–	1	–	–	–
	Nov.	–	2	–	–	–
	Dec.	–	–	–	–	–
1982	Jan.	–	–	–	–	–
	Feb.	–	–	–	1	–
	Mar.	3	5	6	32	26‡
	Apr.	13	17	9	–	–
	May	–	–	–	–	–
	June	–	–	–	–	–

*The Kimhae and Kunsan strains of *P. manchouricus* and the Gongju strain of *G. misella* had 10 males and 10 females in each aquarium.

†Fifteen (five males and 10 females) German snails of *B. tentaculata* were cultured in an aquarium.

‡Only one female snail of the Portuguese strain of *B. tentaculata* was obtained originally. It laid two egg masses in August 1981, from which a total of seven snails (two males and five females) hatched.

‡Egg masses laid by the offspring of the original snail.

and, although one or two egg masses were found sporadically in October and November 1981, the majority of their egg masses were found from March through April of the next year.

The snails of the Gongju strain of *Gabbia misella* were placed in conventional aquaria in September 1981. The egg masses were found from March through April 1982, similar to that observed for *Parafossarulus manchouricus*.

The German and Portuguese strains of *Bithynia tentaculata* exhibited the same trend as the other bithyniids, i.e., they laid the majority of their eggs in March of the next year (Table 4). The incubation period of these eggs at room temperature was about two weeks (Table 5). The Portuguese strain of *B. tentaculata* was started with only one female, which presumably had mated before leaving Portugal. This female laid two egg masses one month after its culture was started. From these egg masses, a total of seven snails (two males and five females) hatched. These offspring laid a total of 26 egg masses in March of the next year (Table 4).

TABLE 5. Comparison of eggs laid in laboratory aquaria by *Parafossarulus manchouricus*, *Gabbia misella* and *Bithynia tentaculata*.

Character	*P. manchouricus* (Kunsan strain)	*G. misella*	*B. tentaculata* (Michigan strain)
Size (maximum length)	1.29 mm ± 0.07	1.06 mm ± 0.04*	1.38 mm ± 0.50
Total number of eggs measured for determining size	30 eggs from 10 egg masses	50 eggs from 10 egg masses	20 eggs from 5 egg masses
Range of the number of eggs per egg mass	4-44	5-23	6-48
Incubation period (days) for hatching at room temperature	15-17	20-22	12-14

*Significantly smaller than other eggs ($P < 0.001$).

Three 7-liter glass aquaria were designated for observing natural deaths of snails of the Kimhae strain of *Parafossarulus manchouricus*. Each aquarium contained 10 males and 10 females. Total mortality of these snails was 31.7% during 13 months of cultivation (Table 6).

Twenty-three baby snails hatched from an egg mass of *Parafossarulus manchouricus* (Kunsan, Korea, strain) in October 1981. The width and height of the shells were measured every three days up to day 108 and then measured once a week up to day 192. The baby snails were transferred from the finger bowls to plastic trays at day 24. Two trays were employed; one tray contained 10 young snails, the other 13. The growth curves for these snails are shown in Fig. 4. The shell length of newly hatched snails averaged about 0.9 mm. On day 156, they had reached an average shell length of 9.18 mm and had laid nine egg masses. The young snails grew very fast at the beginning and attained almost full adult size within 54 days. A steady increase in shell sizes was observed until the snails began laying eggs.

The egg laying of the first generation of *Parafossarulus manchouricus* was from April through June 1981, and then stopped. The second generation was cultured in the same manner as the first. The mortality of the young snails was much lower than the field-collected

TABLE 6. Mortality of *Parafossarulus manchouricus* in conventional aquaria.*

Year	Month	Total no. living snails	Cumulative % mortality
1981	May	60	0
	June	58	3.3
	July	57	5.0
	Aug.	57	5.0
	Sep.	55	8.3
	Oct.	53	11.7
	Nov.	50	16.7
	Dec.	50	16.7
1982	Jan.	45	25.0
	Feb.	45	25.0
	Mar.	44	26.7
	Apr.	42	30.0
	May	41	31.7
	June	41	31.7

*Three aquaria (7 liters of culture water per aquarium; 350 ml of water per snail) were designated for observing age-related mortality of the Kimhae strain of *P. manchouricus*. Each aquarium contained a total of 20 snails (10 males, 10 females).

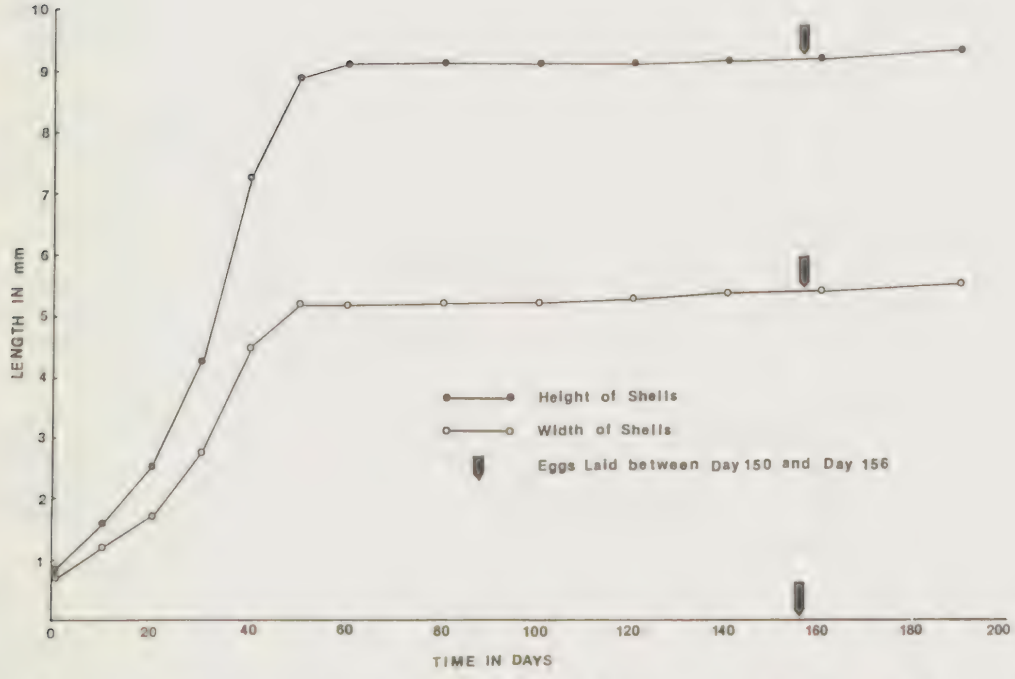


FIG. 4. Growth curves of the first generation (F_1) of *Parafossarulus manchouricus* (Kunsan, Korea, strain).

parent snails. During 10 months of cultivation, only one out of 23 young snails had died (4.3% mortality) (Table 7).

TABLE 7. Number of egg masses (F_2) laid by 23 first-generation laboratory-born *Parafossarulus manchouricus* (Kunsan strain).*

Year	Month	Number of egg masses	Number of dead snails (% mortality)
1981	Oct.	–	0
	Nov.	–	0
	Dec.	–	0
1982	Jan.	–	0
	Feb.	–	0
	Mar.	–	0
	Apr.†	9	0
	May	11	1 (4.3%)
	June	10	0
	July	–	0
	Aug.	–	0

*Twenty-three baby snails (eight males and 15 females) from an egg mass of *P. manchouricus* (Kunsan strain) obtained in October 1981 were raised for observing their life cycle.

†Nine egg masses were laid by the first generation of snails between Day 150 and Day 156.

Comparative morphology

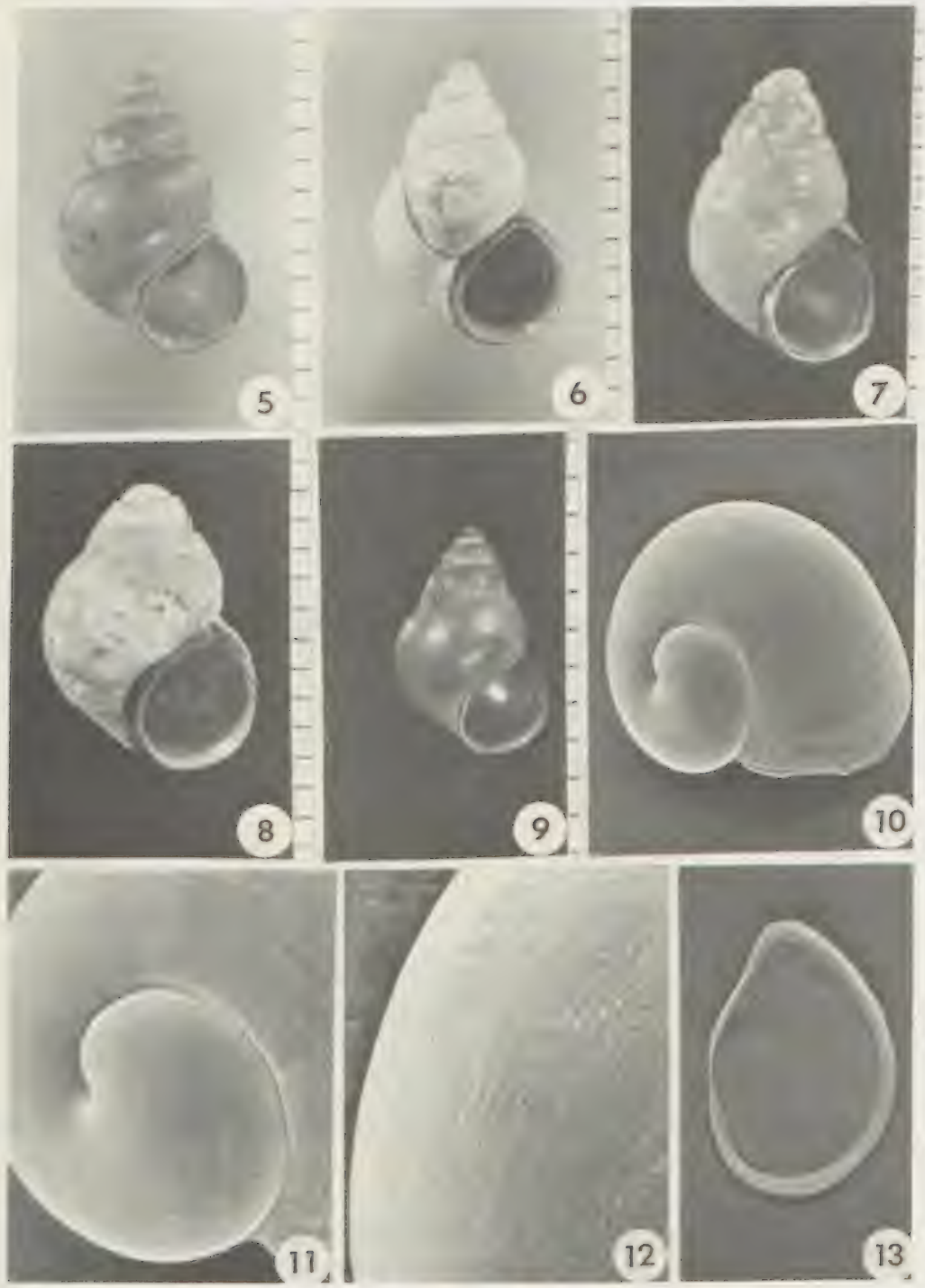
Shells (Figs. 5-12)

The shells of *Parafossarulus manchouricus* are all characterized by having spiral keels (Table 8) and heavily eroded apices, especially in old shells. The lip of the aperture is thickened and, in some individuals, dark brown. The color of adult shells is horn or amber. The maximum length of the shells was 10.8 to 11.7 mm (Figs. 7, 8; Table 9).

The shells of *Gabbia misella* are much smaller than those of the other two species. None of the shells were over 7.12 mm in maximum length (Table 9). The shells of this species are yellowish green (as in *Bithynia tentaculata*), have about five whorls, which are sculptured with fine transverse growth lines and sometimes with very fine spiral lines. The apex of the shell usually is not eroded. The aperture lips are not thickened (Fig. 9; Table 8).

All adult shells of all the specimens of *Bithynia tentaculata* have about five whorls. These are sculptured with fine transverse growth lines (Table 8). The apical whorls of the shells usually are present even in eroded shells (Figs. 5, 6). The aperture lip of the shell has a dark edge. The color of the rest of the adult shell normally is yellowish green. The maximum length of the shells of this species is about 11 mm (Table 9).

A three-day old shell of *Parafossarulus manchouricus* studied with the scanning electron microscope exhibited sculpture of fine growth lines and spiral lines (Figs. 10, 11). A high power magnification of the apical shell sculpture is shown in Fig. 12. This is an enlargement of the apical area of Fig. 11. No specific sculpture in the embryonic whorl of *P. manchouricus* was observed, except for slight spiral wrinkles on the surface. This scanning electron microscopic pattern of the embryonic shell of *P. manchouricus* is distinctly different from that of hydrobiid snails.



FIGS. 5-9. Shells of Bithyniidae. Measurement lines in mm. FIG. 5. *Bithynia tentaculata*, Michigan. FIG. 6. *B. tentaculata*, Michigan, with most of the periostracum and outer ostracum eroded away. A well-developed varix remains. FIG. 7. *Parafossarulus manchouricus*, Kimhae, Korea. FIG. 8. *P. manchouricus*, Kimhae, heavily eroded. FIG. 9. *Gabbia misella*. FIGS. 10-12. SEM photographs of three-day old shell of *P. manchouricus*, Kimhae. Fig. 10, x40; Fig. 11, x68; Fig. 12, x560. Fig. 12 is the part of the shell at the very beginning of the first whorl. FIG. 13. SEM photograph of operculum of three-day old *P. manchouricus*, x56.

TABLE 8. Some morphological characteristics of *Parafossarulus manchouricus*, *Gabbia misella* and *Bithynia tentaculata* employed in this study.

Character	*P. manchouricus*	*G. misella*	*B. tentaculata*
Shell			
Shape	Subovately conic	Ovately conic	Subovately conic
Whorls	Spirally raised ridges with growth lines	Smooth with microscopic growth lines	Smooth with microscopic growth lines
Sutures	Not deeply indented	Deeply indented	Deeply indented
Lip	Thickened and sometimes colored dark brown	Edged	Darkly edged
Apex	Usually eroded	Rather sharp	Rather sharp
Color	Olive-buff*	Deep olive-buff	Deep olive-buff
Size	About 10 mm in adults	About 5-7 mm in adults	About 10 mm in adults
Operculum	Calcareous	Calcareous	Calcareous
	Concentric with paucispiral nucleus	Concentric with paucispiral nucleus	Concentric with paucispiral nucleus
	Cannot be withdrawn into the aperture	Cannot be withdrawn into the aperture	Cannot be withdrawn into the aperture
Animal			
Cup-shaped skin flap on the side of neck just behind the right tentacles	Present	Present	Present
Pigment granules on the head-foot	Pale olive-buff*	Orange chrome	Pale olive-buff
Color pattern of mantle	Transparent, whitish with gray-black mottlings of varying pattern	Translucent with sparse, black cobwebby mottlings	Transparent, whitish with gray-black mottlings of varying pattern
Verge in male	Bifid	Bifid	Bifid
Radular formulae	2:1:1:1:2	2:1:1:1:2	2:1:1:1:2

*Color of the shell and the pigment granules on the head-foot of the snails follows the nomenclature of Ridgway (1912).

Table 9 presents data on relative spire height [RSH] and sculptural rank of the species of Bithyniidae studied here. All pairs of species and populations were significantly different ($P < 0.05$) with respect to relative spire height, except for two of the Korean populations (Haman and Chongpyung) and Korean (Haman and Chongpyung) versus Japanese populations of *Parafossarulus manchouricus* (although the sculptural rank of the Japanese population was higher than that of the Korean bithyniids). On the other hand, the RSH values between the Korean populations and the Taiwanese population of *P. manchouricus* were significantly different ($P < 0.001$ in Chongpyung, Korea/Taiwan populations, and $P < 0.005$ in Haman, Korea/Taiwan populations). Additionally, the Taiwanese population had the highest

TABLE 9. Shell characteristics of *Parafossarulus manchouricus*, *Gabbia misella* and *Bithynia tentaculata*.

Species	n	Range of aperture length (mm)	Range of shell length (mm)	RSH		SR
				Range	Mean ± S.D.	
P. manchouricus						
Haman strain	20	4.44-5.80	9.06-11.66	1.81-2.15	2.01 ± 0.09	2
Chongpyung strain	20	4.76-5.52	9.39-10.91	1.91-2.07	1.99 ± 0.04	2
Japan strain	16	4.27-5.25	9.10-10.80	1.92-2.25	2.06 ± 0.08	3
Taiwan strain	20	4.45-5.76	9.61-11.60	1.85-2.23	2.09 ± 0.10	4
G. misella	17	2.77-3.42	5.41-7.12	1.95-2.24	2.05 ± 0.07	1
B. tentaculata						
Michigan strain	20	4.38-5.14	8.74-11.06	1.96-2.24	2.08 ± 0.08	1

Abbreviations: n = number of specimens; RSH = relative spire height; SR = sculpture rank (rank 1 = the smoothest of the species being compared [with no spiral keels]; rank 4 = shells with heavy spiral keels).

sculptural rank (4). It is obvious that there are morphological differences among the geographic populations of *P. manchouricus* in terms of relative spire height of the adult shells.

In the populations of *Parafossarulus manchouricus*, Taiwanese snails revealed the greatest RSH value (2.09 ± 0.10) and the highest sculptural rank (4) among those populations which had values that were significantly different from the Korean populations. And, since the Taiwanese population has a greater spire height, it therefore has a smaller apertural perimeter.

Opercula (Figs. 13-19)

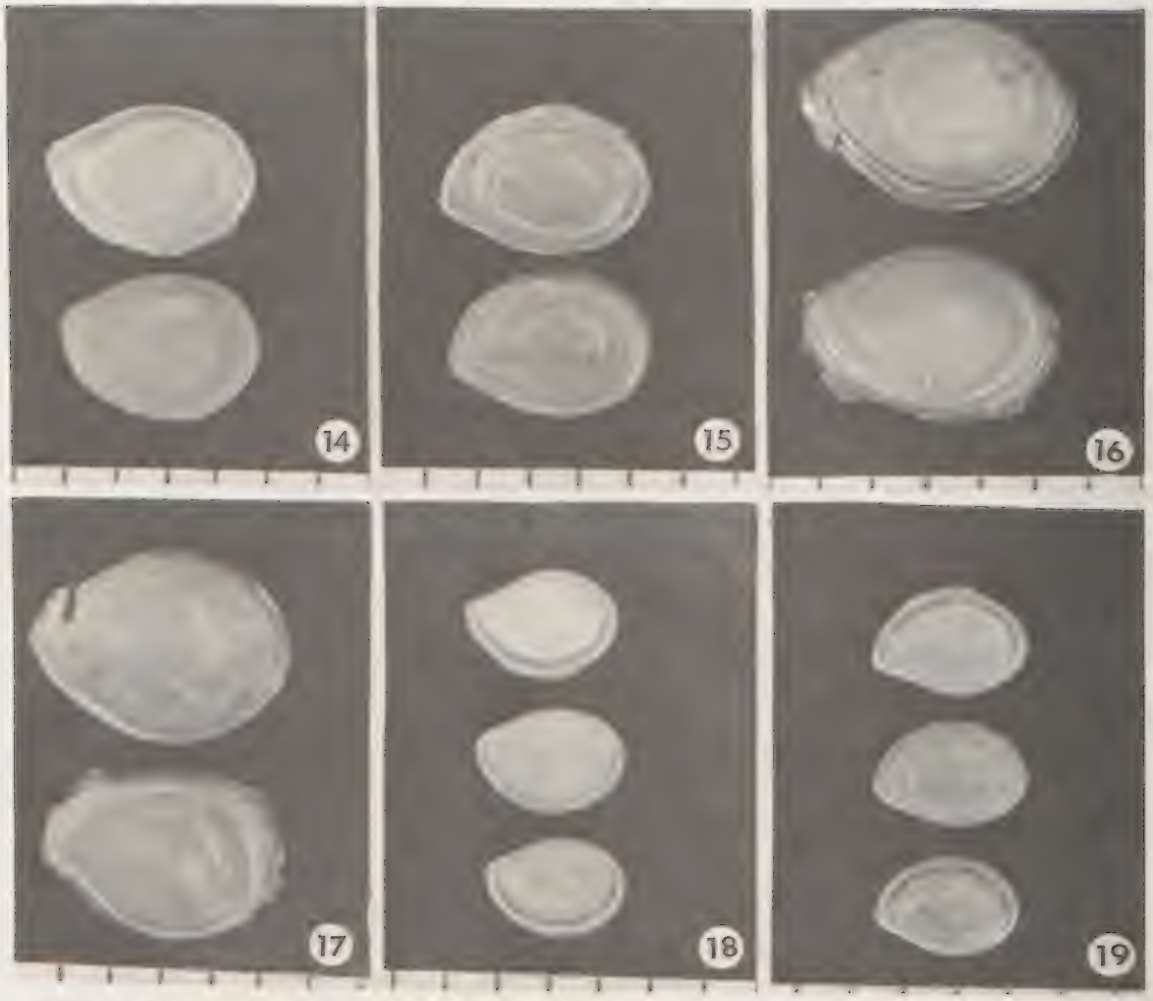
The opercula in all the bithyniid species used in this study were calcareous and concentric with a paucispiral nucleus. The operculum of a newly hatched (three-day old) *Parafossarulus manchouricus* consists almost entirely of the paucispiral nucleus (Fig. 13). Its margin is thickened with calcareous material. The inner sides of the young and old opercula are flat and lack sculpture (Figs. 14-19). Among individuals of the various species, there are variations in sizes of the opercula. But, in none of the species of bithyniid snails observed here can the opercula be withdrawn inside the shells' body whorls (a character which differentiates the Bithyniidae from the Hydrobiidae). That is, the various opercula match exactly the sizes of the respective shell apertures (peritremes) into which they fit. *Gabbia misella*, the smallest species I studied, had the smallest opercula.

Mantle pigmentation (Figs. 20-22)

The mantle pigment patterns in the juvenile snails of *Parafossarulus manchouricus*, *Gabbia misella* and *Bithynia tentaculata* were observed under the dissecting microscope and drawn with the aid of a camera lucida. The patterns were characteristic in each species. The mantle of *B. tentaculata* is pigmented with dense, black mottling without any apparent order (Fig. 20). In *P. manchouricus*, there are three to four parallel spiral rows of black mantle pigment (Fig. 21). The mantle of *G. misella* is pigmented with "sparse, black cobwebby mottlings" as described by Abbott (1948) (Fig. 22).

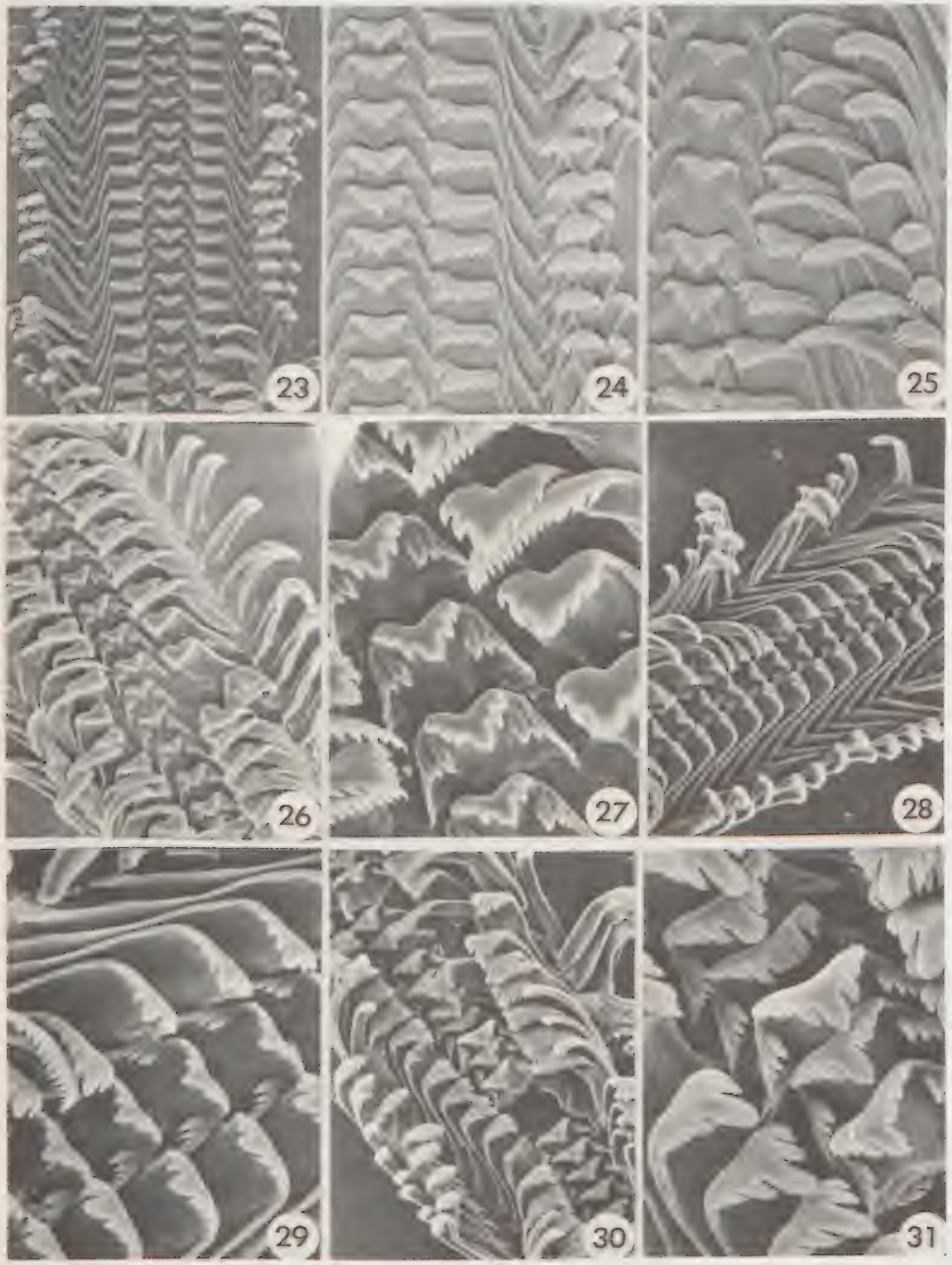
Radulae (Figs. 23-34)

Scanning electron microscopy on the radulae of *Parafossarulus manchouricus* (Kimhae,

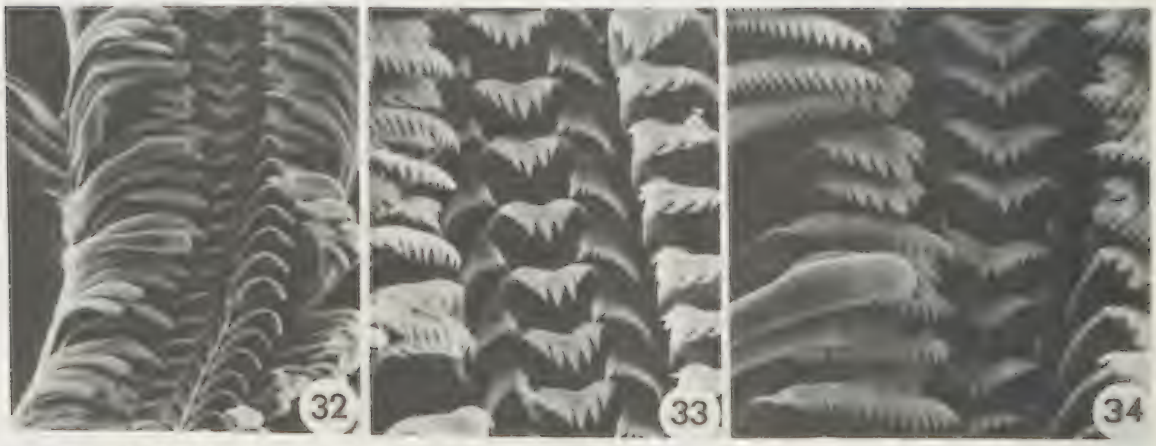


FIGS. 14, 15. Opercula of *Bithynia tentaculata*, Michigan. Fig. 14, inner side; Fig. 15, outer side. FIGS. 16, 17. Opercula of *Parafossarulus manchouricus*, Kimhae, Korea. Fig. 16, inner side; Fig. 17, outer side. FIGS. 18, 19. Opercula of *Gabbia misella*. Fig. 18, inner side; Fig. 19, outer side. Measurement lines in mm.

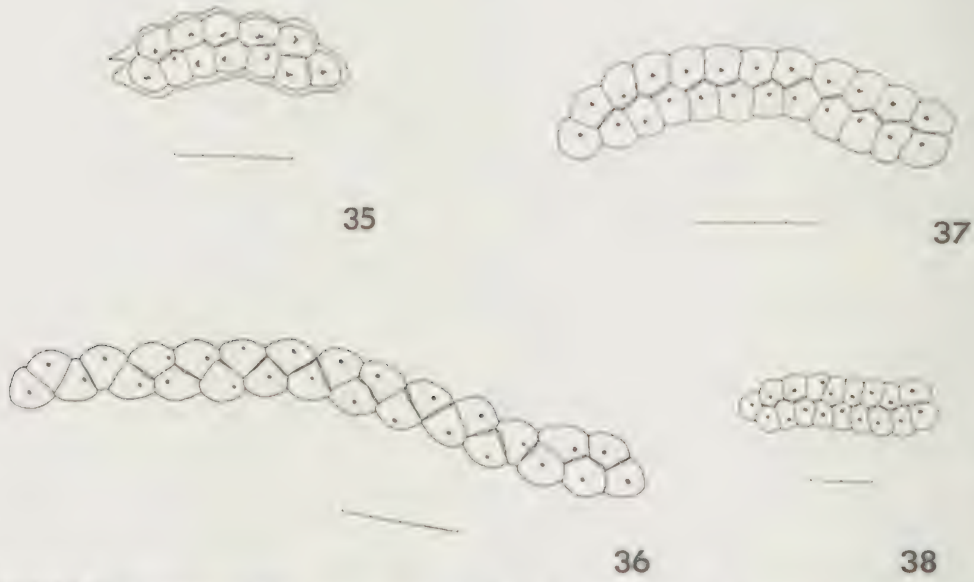
FIGS. 20-22. Mantle pigment patterns of Bithyniidae. FIG. 20. *Bithynia tentaculata*, Michigan. FIG. 21. *Parafossarulus manchouricus*, Kunsan, Korea. FIG. 22. *Gabbia misella*. Measurement lines in mm.



FIGS. 23-31. SEM photographs of radulae of Bithyniidae. FIGS. 23-25. *Parafossarulus manchouricus*, Kimhae, Korea. Fig. 23, x113; Fig. 24, x226; Fig. 25, x282. FIGS. 26, 27. *P. manchouricus*, Taiwan. Fig. 26, x140; Fig. 27, x424. FIGS. 28, 29. *Bithynia tentaculata*, Michigan. Fig. 28, x170; Fig. 29, x480. FIGS. 30, 31. *B. tentaculata*, Germany. Fig. 30, x140; Fig. 31, x424.



FIGS. 32-34. Radulae of *Gabbia misella*. Fig. 32, x180; Fig. 33, x490; Fig. 34, x490.



FIGS. 35-38. Egg masses of Bithyniidae. FIG. 35. *Parafossarulus manchouricus*, Haman, Korea. FIG. 36. *P. manchouricus*, Kunsan, Korea. FIG. 37. *Bithynia tentaculata*, Michigan. FIG. 38. *Gabbia misella*. Measurement lines in mm.

Korea, and Taiwan strains), *Gabbia misella* (Gongju, Korea) and *Bithynia tentaculata* (Michigan and German strains) was carried out to discern the fine morphology of the radulae to see if they had any taxonomically useful characters. The radular formula of all the bithyniid snails studied was 2:1:1:1:2. The central teeth were all multicuspid and had numerous basal denticles. The lateral teeth also were multicuspid and, like the marginal teeth, lacked basal denticles. The marginals consisted of two teeth on each outer edge of the radula (an inner and an outer tooth). The marginal teeth were slender and also were multicuspid.

The central tooth of *Parafossarulus manchouricus* (Kimhae, Korea) were spade- or arrowhead-shaped, bilaterally symmetrical, with a single larger central cusp and two or (more often) three smaller cusps (progressively smaller distally) on each side. Sometimes one or more of the side cusps exhibited an anomaly by being split into two smaller cusps, and sometimes a

small denticle occurred between two of the cusps. There were two to five basal denticles on each side of the central tooth. These denticles occurred on a ridge near the lateral margins of the teeth. The more median denticle on each side was largest, with the other denticles becoming increasingly smaller distally. The smaller most distal basal cusps often were fused into a bumpy ridge.

The central teeth of the Taiwanese strain of *Parafossarulus manchouricus* were similar to those of the Kimhae, Korea, strain, but the cutting end of the mesocone was nipple-shaped in outline rather than spade-shaped, the basal denticles were much more pronounced, and the third to fifth most distal basal denticles were more often or usually fused.

The central teeth of *Bithynia tentaculata* from Michigan had spade-shaped mesocones, and the teeth were very similar to those of *Parafossarulus manchouricus* (Kimhae, Korea), except that in the one specimen I studied there seemed to be little tendency for the side cusps to split into two cusps. *B. tentaculata* from Germany was basically the same as the above two populations, but with the central teeth sometimes having four cusps on each side of the central cusp.

The central teeth of *Gabbia misella* from Gongju, Korea, differed from those of the above species in several respects, of which the most noticeable were (1) the central cusp (mesocone) was only slightly larger than the flanking cusps (ectocones), (2) there were usually four ectocones on each side of the mesocone, (3) the ridge bearing the basal denticles was more broadly flexed off the lateral margins of the tooth and (4) the bases of the central teeth were relatively wider.

The lateral teeth of *Parafossarulus manchouricus* (Kimhae, Korea) had a broad spade- or arrowhead-shaped mesocone, flanked by three or four shorter and narrower ectocones and three shorter and narrower entocones. On each side of the mesocone, the ectocones and entocones decreased progressively in size distally. In the specimen of the Taiwanese strain of *P. manchouricus*, the mesocone of the first lateral tooth was relatively much broader and, like the mesocone of the central tooth, the cutting edge was nipple-shaped in outline. There were three ectocones and two entocones. The lateral teeth of the Michigan *Bithynia tentaculata* had spade-shaped mesocones with rounded ends, and three ectocones and two mesocones, both types of cusps having pointed ends. In the German *B. tentaculata*, the mesocones were longer than in the other species and populations studied. The cutting edge of the mesocone was slightly pointed or rounded. The mesocone cusps were generally flanked by three ectocones and three entocones. Sometimes two of the ectocones were fused. The lateral teeth of *Gabbia misella* had three or four ectocones and three entocones. The mesocones in one of the specimens were long, spade-shaped or triangular, and were sharply pointed. In the other specimen, the cutting edge of the mesocone was more rounded.

The inner marginal teeth of *Parafossarulus manchouricus* (Kimhae, Korea, and Taiwan) and *Bithynia tentaculata* (Michigan and German strains) had about 15 cusps, all nearly of equal size. Some of the more distal cusps had a tendency to fuse. Very little difference could be seen in the inner marginal teeth of these four populations. The inner marginals of *Gabbia misella* also were very similar, except that there were several more cusps, and there seemed to be less tendency for some of the cusps to fuse.

The outer marginals were more slender than the inner marginals and had fewer cusps (about nine). I did not detect any noticeable differences in the outer marginals between the various species and populations.

In relative sizes, the radulae of *Parafossarulus manchouricus* (Korean and Taiwanese strains) and *Bithynia tentaculata* (Michigan and German strains) did not differ greatly from each other.

Scanning electron micrographs of the radulae of the species and populations studied are shown in Figs. 23-34.

Egg masses (Figs. 35-38)

The eggs of the three species of bithyniid snails studied here were all laid in elongate masses with two rows per mass (Figs. 35-38). The eggs were not surrounded by a common gelatinous matrix, but simply were stuck to each other at their surfaces. Some masses of *Parafossarulus manchouricus* appeared to have a gelatinous margin (e.g., see Fig. 35), but this did not seem to be a constant characteristic. Sometimes the two rows of eggs were strung out in a longer, narrower line (i.e., the mass appeared like an alternating line of eggs) (see Fig. 37), but this was also not a constant characteristic.

The egg masses of *Parafossarulus manchouricus* contained 4-44 eggs, *Bithynia tentaculata* 6-48 eggs and *Gabbia misella* 5-23 eggs (Table 5). The incubation period of the eggs of *G. misella* was approximately three weeks at room temperature (ca. 25°C), which was the longest of the species studied. The eggs of *B. tentaculata* were the largest in size (mean diameter = 1.38 mm), followed by *P. manchouricus* (mean diameter = 1.29 mm), and those of *G. misella* were significantly smaller (mean diameter = 1.06 ± 0.04, $P < 0.001$).

Chromosome cytology

Chromosome cycle (Figs. 39-44)

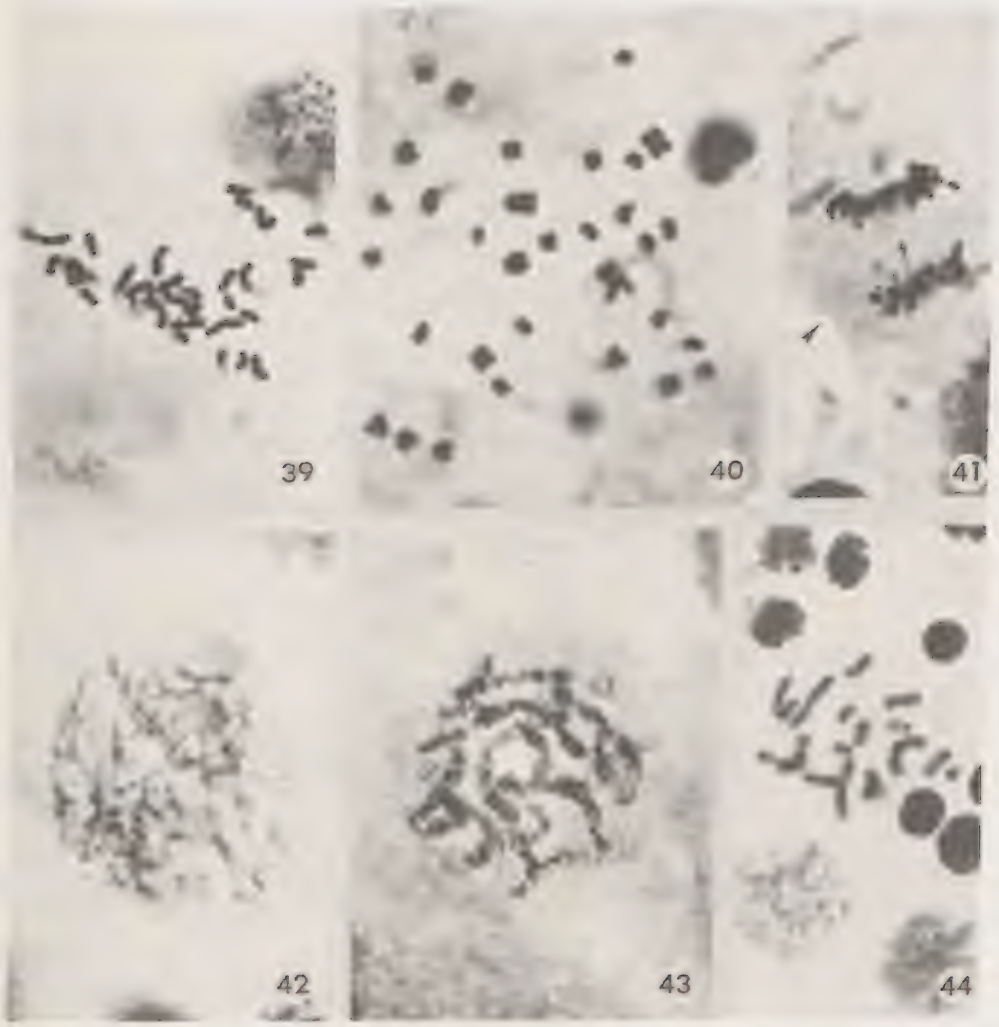
The chromosome cycle was studied mainly from spermatogonial divisions of germ cells in *Parafossarulus manchouricus* (Haman, Korea, strain). Some observations were made as well of chromosomes during female gametogenesis. These same gonadal chromosome stages were observed also in the other bithyniid populations. No specific differences were observed in details of the chromosome cycle in the various species and populations. And no significant differences were observed in the chromosome cycle of these bithyniid snails and the land snail *Catinella vermeta* (Say) as described by Patterson & Burch (1966). Photographs of several stages in the chromosome cycle of *P. manchouricus* are shown in Figs. 39-44.

Chromosome numbers (Figs. 45-47)

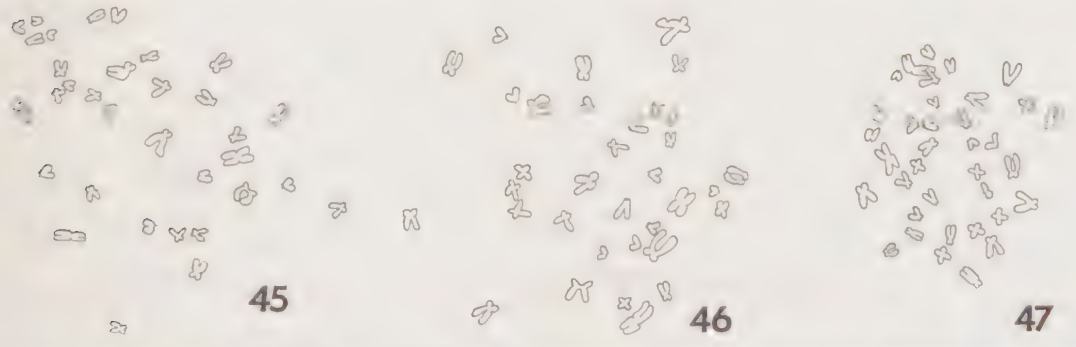
Two different chromosome numbers were observed in the two Korean bithyniid species: n=17 in *Parafossarulus manchouricus* and n=18 in *Gabbia misella* (Table 10). Their diploid chromosome numbers as seen at mitotic metaphase were 34 in *P. manchouricus* and 36 in *G. misella* (Figs. 46, 47). The German and Michigan strains of *Bithynia tentaculata* had 17

TABLE 10. Haploid chromosome numbers reported in the family Bithyniidae.

Species	Locality	Sex of snails studied	Haploid no.	Reference
Parafossarulus manchouricus	Korea	Male and female	17	This study
Gabbia misella	Korea	Male and female	18	This study
Bithynia tentaculata	Germany	Male	17	Ankel, 1924, 1933; Keyl, 1955
	Germany	Male and female	17	This study
	France	Male	17	Tuzet, 1930 (*fide* Butot & Kiauta, 1966)
	Netherlands	Male	17	Butot & Kiauta, 1966
	U.S.A.	Male and female	17	This study
Bithynia leachi	Netherlands	Male	17	Butot & Kiauta, 1966
Bithynia usseriensis	Japan	Male	17	Patterson, 1967
Mysorella costigera	India	?	17	Patterson, 1969



FIGS. 39-44. Chromosomes of *Parafossarulus manchouricus*, Haman, Korea. FIG. 39. Spermatogonial mitotic late prophase. Three chromosomes are out of the optical plane. FIG. 40. Spermatogonial mitotic metaphase. One chromosome is obscured by an artefact. FIG. 41. Spermatogonial anaphase. The arrow points to the cell margin. FIG. 42. Zygonema, with the beginning of synapsis of the homologous chromosomes. FIG. 43. Pachytene bivalent chromosomes. FIG. 44. Haploid monads of Telophase II. All Figs. x1730.



FIGS. 45-47. Camera lucida drawings of spermatogonial mitotic metaphase chromosomes. x1650. FIG. 45. *Bithynia tentaculata*, Michigan. FIG. 46. *Parafossarulus manchouricus*, Haman, Korea. FIG. 47. *Gabbia misella*.

bivalents during the first meiotic division, and 34 chromosomes were observed during both spermatogonial and oögonial divisions (Fig. 45).

Karyology (Figs. 48-55)

The chromosomes in male and female mitotic metaphase cells were karyotyped for analysis of chromosome morphologies in the three species of bithyniid snails. The chromosome configurations were made directly from photographs of single cells, with the help of camera lucida drawings made of the actual chromosomes. All the chromosomes compared during the course of these studies were from photographs of the same magnification.

Each cell of *Parafossarulus manchouricus* studied had 34 chromosomes: three metacentric, nine submetacentric and five acrocentric pairs (Table 11; Fig. 50). All cells of *Bithynia tentaculata* had a chromosome number of 34. Fig. 48 shows a representative karyotype of the Michigan strain of *B. tentaculata*. The largest pair of chromosomes are metacentric, the second through tenth are submetacentric, and the remaining seven are acrocentric. The German strain of *B. tentaculata* had three metacentric, 10 submetacentric and four acrocentric chromosome pairs (Fig. 49). The cells of *Gabbia misella* had a mitotic chromosome number of 36. The oögonial metaphase karyotype of this species (Fig. 51) consists of four pairs of metacentric chromosomes, seven pairs of submetacentric chromosomes and seven pairs of acrocentric chromosomes.

TABLE 11. Characterization of the chromosomes of *Parafossarulus manchouricus*, *Gabbia misella* and *Bithynia tentaculata*.

Species	No. of snails studied	Haploid number of chromosomes			
		Metacentric	Submetacentric	Acrocentric	Total
P. manchouricus Haman strain	24	3	9	5	17
G. misella	10	4	7	7	18
B. tentaculata					
Michigan strain	15	1	9	7	17
German strain	6	3	10	4	17

The mitotic metaphase chromosome sizes ranged from 2.88 μm to 0.79 μm in *Parafossarulus manchouricus* and from 2.80 μm to 0.83 μm in *Gabbia misella* (Table 12). The ratios of length between the longest and shortest chromosomes in *P. manchouricus* and *G. misella* were 3.6 and 3.4, respectively. The two largest chromosome pairs of the Michigan and German strains of *Bithynia tentaculata* were 2.20 μm and 2.76 μm, respectively, and the two smallest pairs were 1.05 μm and 0.70 μm. The ratios of length between the longest and shortest chromosomes of the Michigan and German strains were 3.1 and 2.6, respectively.

Chromosomal homologies between species of bithyniid snails cannot be established with certainty without banding studies. However, interspecific homologies on the basis of relative length (percent total complement length) were inferred in this study after measuring the chromosome lengths. Table 13 shows the lengths of a haploid chromosome set of each of the three species of bithyniid snails. Relative chromosome lengths were calculated as shown in Table 14. The data indicate that in regard to lengths most chromosome pairs are similar in the Michigan and German populations of *Bithynia tentaculata*, and between *B. tentaculata* and *Parafossarulus manchouricus*, although the relative length of the last chromosome pair

FIGS. 48-51. Mitotic metaphase chromosomes of Bithyniidae. The chromosomes of each species are arranged in horizontal rows according to the positions of their centromeres: metacentrics in the top row, submetacentrics in the middle row, and subacro- and acrocentric chromosomes in the bottom row. FIG. 48. *Bithynia tentaculata*, female, Michigan. FIG. 49. *B. tentaculata*, female, Germany. FIG. 50. *Parafossarulus manchouricus*, male, Haman, Korea. FIG. 51. *Gabbia misella*, female.

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FIGS. 52-55. Schematic representation of the karyotypes of Bithyniidae. m = Metacentric, s = submetacentric, and a = subacro- or acrocentric chromosomes. FIG. 52. *Bithynia tentaculata*, Michigan. FIG. 53. *B. tentaculata*, Germany. FIG. 54. *Parafossarulus manchouricus*, Haman, Korea. FIG. 55. *Gabbia misella*.

TABLE 12. Length of chromosomes (μm) in *Parafossarulus manchouricus, Gabbia misella* and *Bithynia tentaculata*.*

Chromosome	*P. manchouricus*	*G. misella*	*B. tentaculata*	
	Haman		Michigan	Germany
1	2.88 ± 0.49	2.80 ± 0.42	2.20	2.76 ± 0.35
3	1.48 ± 0.72	1.38 ± 0.03	2.00	1.33 ± 0.49
5	1.15 ± 0.65	1.25 ± 0.07	1.70	1.22 ± 0.42
7	2.76 ± 0.81	1.20 ± 0.14	1.62	2.17 ± 0.49
9	2.20 ± 0.58	1.89 ± 0.16	1.40	2.05 ± 0.35
11	2.05 ± 0.44	1.77 ± 0.09	1.30	1.61 ± 0.07
13	1.73 ± 0.48	1.70 ± 0.14	1.22	1.50 ± 0.25
15	1.58 ± 0.63	1.52 ± 0.11	1.18	1.48 ± 0.14
17	1.40 ± 0.70	1.45 ± 0.07	1.10	1.47 ± 0.21
19	1.31 ± 0.52	1.40 ± 0.14	0.96	1.41 ± 0.63
21	1.24 ± 0.42	1.20 ± 0.28	1.24	1.28 ± 0.14
23	1.15 ± 0.65	1.82 ± 0.03	1.22	1.20 ± 0.70
25	1.59 ± 0.39	1.44 ± 0.19	1.20	1.11 ± 0.63
27	1.38 ± 0.34	1.31 ± 0.27	0.98	1.54 ± 0.28
29	1.23 ± 0.85	1.12 ± 0.11	0.80	1.40 ± 0.41
31	1.10 ± 0.41	1.10 ± 0.14	0.80	1.25 ± 0.35
33	0.79 ± 0.33	0.90 ± 0.14	0.70	1.05 ± 0.35
35	–	0.83 ± 0.09	–	–

*Measurements were made from four sets of chromosomes in *P. manchouricus*, two sets in *G. misella* and the German strain of *B. tentaculata*, and one set in the Michigan strain of *B. tentaculata*.

TABLE 13. Relative chromosome lengths (μm) in *Parafossarulus manchouricus, Gabbia misella* and *Bithynia tentaculata*.*

Chromosome	*P. manchouricus*	*G. misella*	*B. tentaculata*	
	Haman		Michigan	Germany
1	10.78 ± 0.58	10.71 ± 0.76	10.18	10.65 ± 0.06
2	10.15 ± 0.55	7.37 ± 0.17	9.25	8.42 ± 0.56
3	8.50 ± 0.30	6.95 ± 0.40	7.86	7.94 ± 0.11
4	7.22 ± 0.56	6.73 ± 0.28	7.49	6.24 ± 0.08
5	6.39 ± 0.29	6.52 ± 0.01	6.48	6.16 ± 0.18
6	6.08 ± 0.43	5.83 ± 0.04	6.01	5.81 ± 0.11
7	5.73 ± 0.24	5.71 ± 0.03	5.74	5.81 ± 0.11
8	5.66 ± 0.22	5.57 ± 0.18	5.64	5.81 ± 0.11
9	5.33 ± 0.31	5.37 ± 0.12	5.64	5.62 ± 0.06
10	4.92 ± 0.09	5.37 ± 0.10	5.55	5.27 ± 0.10
11	4.68 ± 0.09	5.19 ± 0.15	5.46	5.04 ± 0.11
12	4.62 ± 0.15	5.11 ± 0.25	5.09	4.96 ± 0.01
13	4.43 ± 0.22	4.46 ± 0.15	4.53	4.81 ± 0.12
14	4.35 ± 0.26	4.29 ± 0.08	4.44	4.69 ± 0.18
15	4.25 ± 0.28	4.21 ± 0.19	3.70	4.45 ± 0.18
16	3.99 ± 0.16	4.03 ± 0.06	3.70	4.29 ± 0.40
17	2.99 ± 0.15	3.44 ± 0.27	3.24	4.06 ± 0.18
18	–	3.18 ± 0.12	–	–

*The chromosome pairs of the karyotypes are arranged by size and are expressed in relative chromosome lengths (absolute chromosome length/total length of haploid complement) x 100 (Paris Conference, 1972).

(the 17th) of *P. manchouricus* is a little smaller than that of the German strain of *B. tentaculata*. *Gabbia misella* is obviously different from the other two species of bithyniids in terms of the chromosome number. The haploid chromosome number of *G. misella* is n=18, in contrast to the haploid number n=17 of the other bithyniid species.

It is interesting that differences in centromere positions occur between the two populations of *Bithynia tentaculata* studied. Only one metacentric chromosome pair was observed in the Michigan strain, whereas three pairs of metacentric chromosomes were found in the German strain. Similarly, the numbers of submetacentric and acrocentric chromosome pairs between the two populations were different. The numbers of submetacentric pairs in the Michigan and German populations were nine and ten, and the acrocentric pairs were seven and four, respectively.

The idiograms of the karyotypes of the three species of bithyniid snails studied here are shown in Figs. 52-55.

Allozyme electrophoresis

Horizontal starch gel electrophoresis (Figs. 56-66)

Thirteen different kinds of enzymes were investigated in this electrophoretic study. The success of detecting enzymatic activities in the four different buffer systems employed is shown in Table 3. Buffer systems I and II usually were used for all the enzyme tests, except for 6-phosphogluconate dehydrogenase activity, and buffer systems III and IV were used only for some tests. Of the four systems, buffer system I gave the best overall results. The dehydrogenases, xanthine oxidase and D-amino acid oxidase activities were poorly discerned from frozen snail samples, so live snails were used in buffer systems I or II, which gave satisfactory results. Buffer systems I, II or III were found to be excellent in testing for glutamate-oxaloacetate transaminase activity, although system I was the best. For non-specific esterase activity, the use of α-naphthyl acetate as the substrate was more appropriate than the use of α-naphthyl butyrate and α-naphthyl propionate in both buffer systems I and II. Buffer systems I and IV were excellent for the detection of alkaline phosphate activity, while buffer system II was excellent for the detection of acid phosphatase activity. Buffer systems I and II both were excellent for resolving alanine aminopeptidase activity, and buffer system II was excellent for the detection of leucine aminopeptidase activity.

The results of electrophoretic analyses are given in Table 14. Scoring of the gels followed the criteria of Ayala et al. (1973). The abbreviations of enzymes are used to symbolize the genes (or loci) coding for the enzymes. When several zones of activity exist for a given enzyme, a hyphenated numeral is added to the symbol of the enzyme to designate each zone and the gene coding for it. The zone of activity with the farthest migration toward the anodal end is designated 1, the next one is designated 2, and so on. Gels were scored as autosomal loci with co-dominant alleles. The most common allele, or electromorph, for each locus was designated with the superscript ^{100}; all other alleles were designated by adding to or subtracting from 100 the number of millimeters by which the migration of the enzyme coded by the allele differs from the standard.

The frequency of an allele was given by

$$\frac{2 H_o + H_e}{2N}$$

where H_o = the number of homozygotes for that allele, H_e = the number of heterozygotes for that allele, and N = the number of individuals examined. The heterozygosity per locus (H_L) was calculated as

$$H_L = 1 - \Sigma x_i^2$$

where x_i = the frequency of the ith allele at a locus. The mean heterozygosity per locus ($\bar{H}_L$) was the sum of H_L over all loci, including monomorphic loci (where $H_L = 0$), divided by the total number of loci examined (Ferguson, 1980).

Nine out of 13 enzyme activities were employed for the electrophoretic assay in this study, and 16 loci from nine enzymes were detectable. A locus was considered polymorphic when no allele had a frequency greater than or equal to 0.95. The number of alleles per locus varied from one (monomorphic) to four (at the EST-5 locus). Allelic variations among the species or among the populations in the same species of snails were found at seven out of 16 (43.8%) loci studies. They were GOT, AlP-1, AlP-2, AcP-2, AAP, EST-4, EST-5. The genetic variation (average heterozygosity) in *Parafossarulus manchouricus* ranged from 0.13 to 0.19 and from 0.07 to 0.10 in *Bithynia tentaculata*, and was 0.06 in *Gabbia misella*. *P. manchouricus* snails were more variable than were the other two bithyniid species (Table 14).

No allelic variation among eight populations of bithyniids used was observed at the following eight monomorphic loci: AlP-3, AcP-1, LAP, EST-1, EST-2, EST-3, XO and β-HBDH. The α-GPDH locus also showed monomorphic bands with the same electrophoretic mobilities in the populations of *Bithynia tentaculata*, but could not be detected in the populations of *Parafossarulus manchouricus* and *Gabbia misella*. Also the AlP-2 and AlP-3 loci were found to be sex related in *P. manchouricus*; that is, the electromorphs of these two loci were always detectable only in the females of *P. manchouricus*, but not in the females or males of other bithyniids employed in this study (Table 14).

D-amino acid oxidase showed no acitivity in buffer systems I and II in this study, possibly because this enzyme was not present, but more probably because our techniques failed to reveal it. 6-phosphogluconate dehydrogenase activity was checked once in buffer system III, and a non-satisfactory result was obtained. Resolution of malate dehydrogenase activity was poor on buffer systems I and II. Streaking rendered many samples uninterpretable. Sorbitol dehydrogenase activity was resolved in buffer system I, but it is not recorded in this study because the number of enzymatic experiments had to be restricted to those which could be done within the budget and time available.

The other nine enzymes showed varying degrees of activity and the following observations of individual enzymatic activities were made in order to give further details.

α-glycerophosphate dehydrogenase [α-GPDH], buffer systems I and II. A single locus which stained strongly was demonstrated in the three populations of *Bithynia tentaculata*. The bands showed all the same electrophoretic mobilities. However, no activity was detected in *Parafossarulus manchouricus* and *Gabbia misella*, even in fresh specimens. Slow monomorphic bands which stained negatively, and which showed up white on the gel, were detected in all three bithyniid species used (Fig. 56).

β-hydroxybutyrate dehydrogenase [β-HBDH], buffer system I. Two monomorphic loci were recognized in the three species of bithyniid snails; no differences were detected among the three species. Three negatively stained monomorphic bands also were observed. The resolution for β-HBDH activity was generally poor, except in one zone (β-HBDH-1).

Xanthine oxidase [XO], buffer system I. XO activity was seen clearly in the preparations made with fresh extracts of snails in buffer system I. A single zone was observed in the three bithyniid species tested, without any electromorphic difference (monomorphic) being detected among the three species.

Glutamate-oxaloacetate transaminase [GOT], buffer system I, II and III. In all populations of *Parafossarulus manchouricus* except the Chongpyung, Korea, population, only single fast-banded individuals (GOT^{100}) were found (Chung & Burch, 1983). The Chongpyung population had individuals with the same fast band as the other populations, but some individuals had a slow band (GOT^{97}), and yet other snails had three bands – fast, slow and intermediate bands. The GOT^{97} allozyme occurring in the Chongpyung population was not detected in the other populations, not even in the Haman population. These electromorphs of

TABLE 14. Allozyme frequencies and average heterozygosities for *Parafossarulus manchouricus*, *Gabbia misella* and *Bithynia tentaculata*.

Locus	Allozyme (allele)	*P. m.* Haman	*P. m.* Chongp.	*P. m.* Japan	*P. m.* Taiwan	*G. m.* Gongju	*B. t.* Mich.	*B. t.* Ger.	*B. t.* Port.
GOT	103	–	–	0.12	–	–	1.00	1.00	1.00
	100	1.00	0.52	0.88	1.00	1.00	–	–	–
	97	–	0.48	–	–	–	–	–	–
	n	31	43	16	25	20	30	20	16
	h	0	0.49	0.21	0	0	0	0	0
AlP-1	100	0.84	0.92	0.59	0.58	–	–	–	–
	97	0.16	0.08	0.41	0.42	0.63	0.60	0.60	0.22
	95	–	–	–	–	0.37	0.40	0.40	0.78
	n	35	38	16	25	20	30	20	16
	h	0.27	0.15	0.48	0.49	0.47	0.48	0.48	0.34
AlP-2 (♀)	100	1.00	1.00	–	0.55	–	–	–	–
	98	–	–	1.00	0.45	–	–	–	–
	n	20	19	8	10	20 (♀+♂)	15	11	4
	h	0	0	0	0.49	–	–	–	–
AlP-3 (♀)	100 (–)	1.00	1.00	1.00	1.00	–	–	–	–
	n	20	19	8	10	20 (♀+♂)	15	11	4
	h	0	0	0	0	–	–	–	–
AcP-1	100	1.00	1.00	1.00	1.00	1.00	ND	1.00	1.00
	n	27	20	16	22	20	12	12	15
	h	0	0	0	0	0	–	0	0
AcP-2	104	–	–	–	–	–	–	0.04	0.04
	102	0.46	0.30	0.34	0.48	1.00	0.50	0.38	0.08
	100	0.54	0.70	0.66	0.52	–	0.50	0.58	0.88
	n	27	20	16	22	20	12	12	12
	h	0.49	0.42	0.45	0.49	0	0.50	0.52	0.22
AAP	100	0.40	0.63	0.73	0.75	1.00	1.00	1.00	1.00
	98	0.60	0.37	0.27	0.25	–	–	–	–
	n	20	12	11	8	20	20	10	10
	h	0.48	0.46	0.39	0.38	0	0	0	0
LAP	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	n	24	15	14	15	20	20	10	10
	h	0	0	0	0	0	0	0	0

TABLE 14. (Continued)

Locus	Allozyme (allele)	*P. m.* Haman	*P. m.* Chongp.	*P. m.* Japan	*P. m.* Taiwan	*G. m.* Gongju	*B. t.* Mich.	*B. t.* Ger.	*B. t.* Port.
EST-1	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	n	27	25	16	22	20	30	20	16
	h	0	0	0	0	0	0	0	0
EST-2	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	n	27	25	16	22	20	30	20	16
	h	0	0	0	0	0	0	0	0
EST-3	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	n	27	25	16	22	20	30	20	16
	h	0	0	0	0	0	0	0	0
EST-4	104	0.35	0.60	0.13	0.34	0.15	–	–	0.53
	102	–	–	–	–	–	–	0.28	–
	100	0.65	0.40	0.87	0.66	0.85	1.00	0.72	0.47
	n	27	25	16	22	20	30	20	16
	h	0.46	0.48	0.23	0.45	0.26	0	0.40	0.49
EST-5	100	0.83	0.88	0.44	0.50	–	–	–	–
	98	0.17	0.12	0.56	0.50	–	–	–	–
	96	–	–	–	–	0.04	1.00	1.00	1.00
	94	–	–	–	–	0.96	–	–	–
	n	12	17	16	22	25	30	20	16
	h	0.28	0.21	0.49	0.50	0.08	0	0	0
XO	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	n	20	20	16	20	20	20	20	16
	h	0	0	0	0	0	0	0	0
α-GPDH	100	ND	ND	ND	ND	ND	1.00	1.00	1.00
	n	10	10	10	10	10	10	10	10
	h	–	–	–	–	–	0	0	0
β-HBDH-1	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	n	20	20	16	20	20	20	20	16
	h	0	0	0	0	0	0	0	0
	$\bar{H}_L$	0.13	0.15	0.15	0.19	0.06	0.08	0.10	0.07

Remarks: Negatively stained monomorphic bands were observed in α-GPDH and β-HBDH gels. AlP-2 (♀) and AlP-3 (♀) bands were associated only with female snails. 100 (–) = cathodally migrated zone in AlP-3 locus. ND = not detected. n = Number of individuals examined. h = Heterozygosity per locus. $\bar{H}_L$ = average heterozygosity per locus.

GOT are assumed to be encoded by different alleles at the same locus. Therefore, GOT is a dimer on the basis of its banding pattern, and those snails possessing an additional intermediate or hybrid band are heterozygotes.

In *Gabbia misella*, the mobility of the GOT electromorph was identical to the fast band (GOT^{100}) of *Parafossarulus manchouricus*. But, in the *Bithynia tentaculata* populations, the monomorphic single-banded electromorph (GOT^{103}) migrated faster than the fast bands (GOT^{100}) of *P. manchouricus* and *G. misella* (Fig. 57).

Esterase [EST], buffer systems I, II and III. The results of non-specific esterase activities detected with α-naphthyl acetate, α-naphthyl butyrate and α-naphthyl propionate as substrates were distinctive according to the species, or even according to the different populations of a species. However, identical activities also were demonstrated at several loci.

EST-1, EST-2 and EST-3 were composed of a single band, which was common to all three species of bithyniid snails used.

EST-4 contained three bands. The fast band ($EST\text{-}4^{104}$) belonged to the populations of *Parafossarulus manchouricus*, *Gabbia misella* and the Portuguese population of *Bithynia tentaculata* (but they did not occur in the Michigan and German populations of *B. tentaculata*). The medium band ($EST\text{-}4^{102}$) occurred only in the German population of *B. tentaculata*, and the slow band ($EST\text{-}4^{100}$) was common to all three of the bithyniid species. The fast band was population-specific for the Portuguese population, and the medium band was specific for the German population of *B. tentaculata* (Fig. 58).

EST-5 was composed of four bands. $EST\text{-}5^{100}$ and $EST\text{-}5^{98}$ bands belonged to the populations of *Parafossarulus manchouricus*; the $EST\text{-}5^{96}$ allozyme band was monomorphic in *Bithynia tentaculata* and common with the fast band of the monomeric electromorphs of *Gabbia misella*; and the slowest band ($EST\text{-}5^{94}$) was observed only in *G. misella* (Fig. 59).

The results also showed quantitative variations in the migrated enzymes in terms of staining intensity of the isozymes encoded by the different loci, i.e., EST-4 and EST-5 allozymes were always more intensive than the others.

A total of seven loci were involved in non-specific esterase activities, but the last two isozymes were resolved so poorly that they were excluded from this study.

Alkaline phosphatase [AlP], buffer systems I, II and IV. Three regions of alkaline phosphatase activity were detected by buffer systems I, II and IV, and these were interpreted as representing the activities of three loci, AlP-1, AlP-2 and AlP-3. Three allozyme electromorphs for AlP-1 were observed; the fast band ($AlP\text{-}1^{100}$) occurred only in the populations of *Parafossarulus manchouricus*, and the slow band ($AlP\text{-}1^{95}$) was detectable only in the populations of *Bithynia tentaculata* and *Gabbia misella*. The medium band ($AlP\text{-}1^{97}$) was common in all three bithyniid species used in this study (Fig. 60).

The allozymes encoded by AlP-2 and AlP-3 loci were all associated with female snails, and were found only in the populations of *Parafossarulus manchouricus*. So, those electromorphs seem to be very specific in regard to sex. Allozymes for AlP-2 migrated anodally and showed dimeric banding patterns. The fast band ($AlP\text{-}2^{100}$) was seen only in Korean populations (Haman and Chongpyung) of *P. manchouricus*, and individual female snails were all homozygous for an allele corresponding to a fast-moving enzyme (F/F), while the slow band ($AlP\text{-}2^{98}$) was detectable only in the Japanese population of *P. manchouricus*, and female individuals were all homozygous for an allele relating to a slow-migrating enzyme (S/S). Heterozygous (F/S) banding patterns for the AlP-2 locus were found only in the Taiwanese population of *P. manchouricus*. A zone of electromorphs encoded by the sex-related AlP-3 locus migrated cathodally and formed monomorphic single bands in the preparations of female snails of *P. manchouricus*, without showing any difference between populations (Figs. 61-65).

Acid phosphatase [AcP], buffer systems I, II, III and IV. Two regions of acid phosphatase activity were detected by buffer systems I, II, III and IV. However, the bands were very diffuse, which sometimes made observations on variation difficult. The first region of the electromorphs (AcP-1) was monomorphic and common to all three bithyniid species used in this

FIG. 56. The enzymatic activities of α-glycerophosphate dehydrogenase in buffer system I of *Gabbia misella, Bithynia tentaculata* and *Parafossarulus manchouricus*. The monomorphic electromorphs were detected only in *B. tentaculata*. A single locus which stained negatively was observed in all three species.

FIG. 57. Schematic representation of GOT band patterns. Note the intrapopulation-specific slow bands in the Chongpyung (Cp) population of *Parafossarulus manchouricus*. The other GOT bands were all monomorphic; in *Gabbia misella* they matched the fast bands occurring in *P. manchouricus*. The monomorphic bands in *Bithynia tentaculata* migrated the farthest toward the anodal end.

FIG. 58. Non-specific esterase activities showing monomeric band patterns for the EST-4 locus in the Portuguese, German and Michigan populations of *Bithynia tentaculata*. The fastest bands occurred only in the Portuguese population. Individual 2 of the Portugal strain is presumed to be a homozygote (S/S) for the slow-moving band, and individual 3 a homozygote (F/F) for the fast-moving band. Other individuals (1, 4, 5 and 6) in the Portuguese strain are heterozygotes (F/S), which contain both bands. Some individuals (1 and 5) in the German population have intermediate bands in the fast and slow banding system; however, the Michigan strain shows only slow-moving electromorphs.

FIG. 59. The non-specific esterase activities for the EST-5 locus in *Gabbia misella, Bithynia tentaculata* and *Parafossarulus manchouricus*.

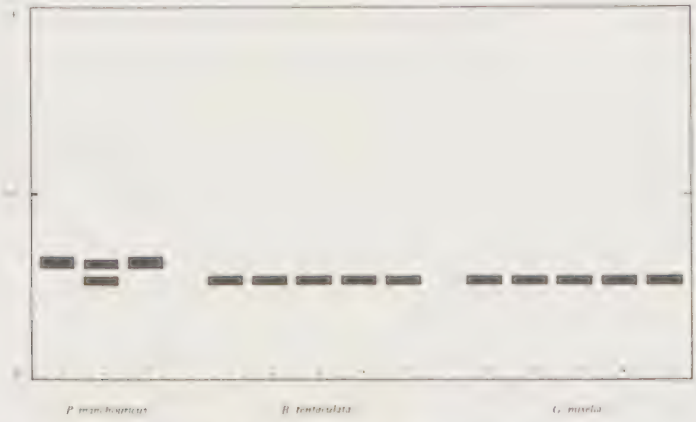

FIG. 60. Enzymatic activities of alkaline phosphatase (AlP-1). The electromorphs of *Bithynia tentaculata* and *Gabbia misella* were matched with the slow band of *Parafossarulus manchouricus* (2), although the enzymatic variation of the bands shown in *B. tentaculata* and *G. misella* is not represented in this figure.

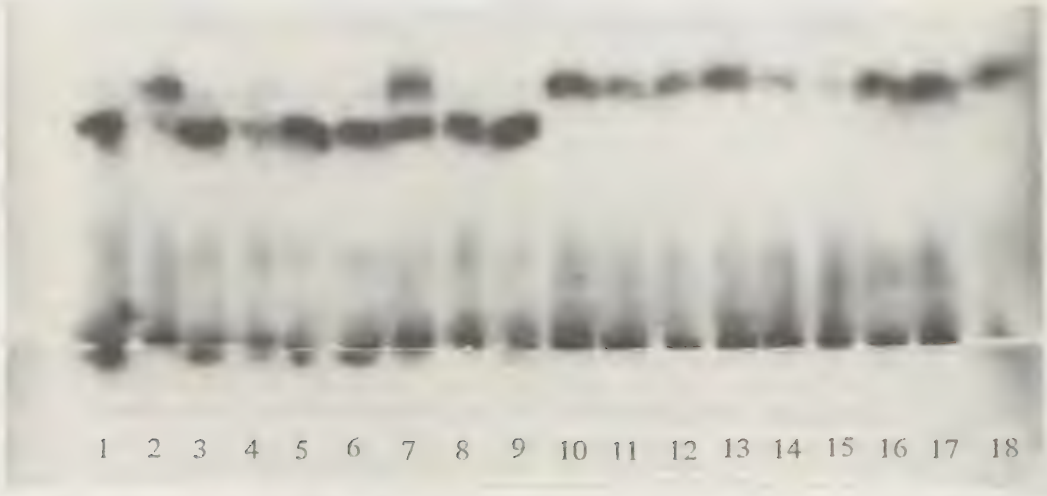

FIG. 61. Enzymatic activities of alkaline phosphatase of the Chongpyung strain of *Parafossarulus manchouricus*. Snails 1-9 (females) have a sex-related slow-moving band, but snails 10-18 (males) lacked this band.

FIG. 62. Enzymatic activities of alkaline phosphatase in the Haman strain of *Parafossarulus manchouricus*. All the electromorphs showing double bands were from female snails.

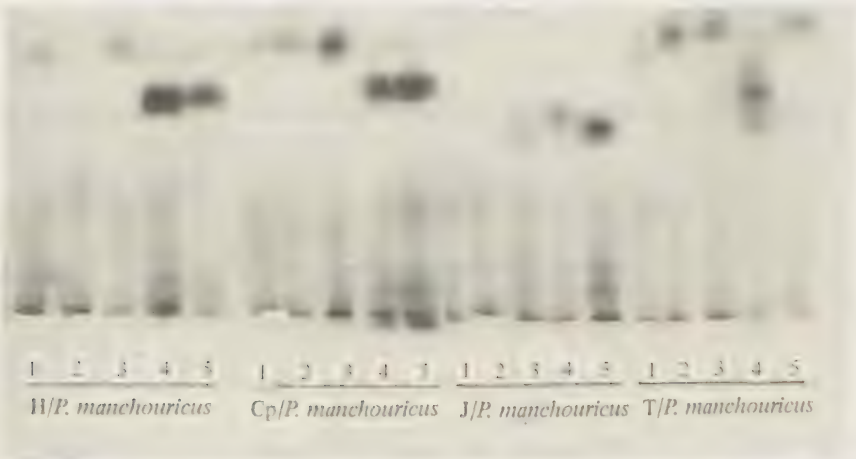

FIG. 63. Alkaline phosphatase activities of the Haman (H), Chongpyung (Cp), Japanese (J) and Taiwanese (T) populations of *Parafossarulus manchouricus*. Note the sex-related AlP-2 and AlP-3 bands in the females. Homozygotes with the fast-moving AlP-2 bands occurred only in the Korean populations (4 and 5 in H; 4 and 5 in Cp) and homozygotes with the slower-moving AlP-3 bands were found only in the Japanese population (3, 4 and 5 in J). Heterozygotes of these two homozygous bands were observed only in the Taiwanese population (4 in T). Female snails (4 and 5) of the Chongpyung strain had cathodally migrating bands. AlP-1 bands in the Japanese population (which occurred in both sexes) were too faint to be seen in this picture.

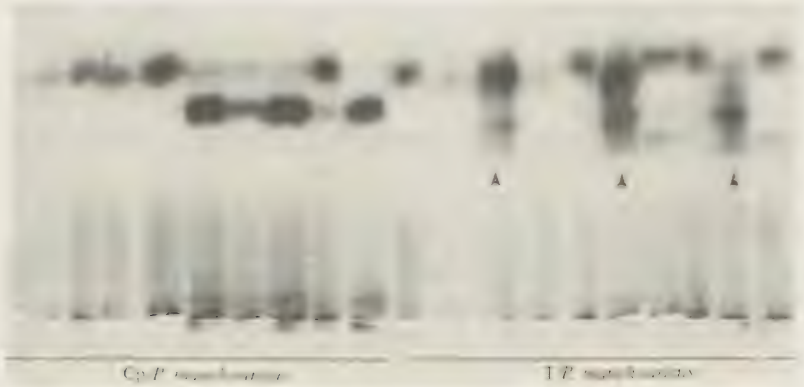

FIG. 64. Alkaline phosphatase activities in ten snails of the Chongpyung (Cp) population and 10 snails of the Taiwanese (T) population of *Parafossarulus manchouricus*. Note the sex-related AlP-2 bands, and in the Taiwanese population the three heterozygous electromorphs (arrows).

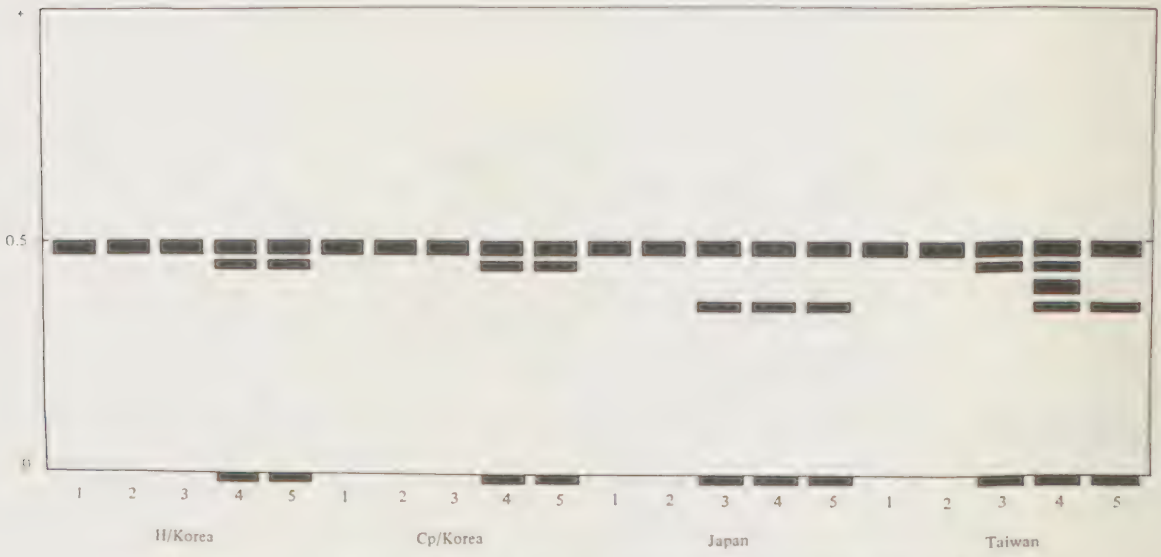

FIG. 65. Schematic representation of alkaline phosphatase activities shown in Fig. 63.

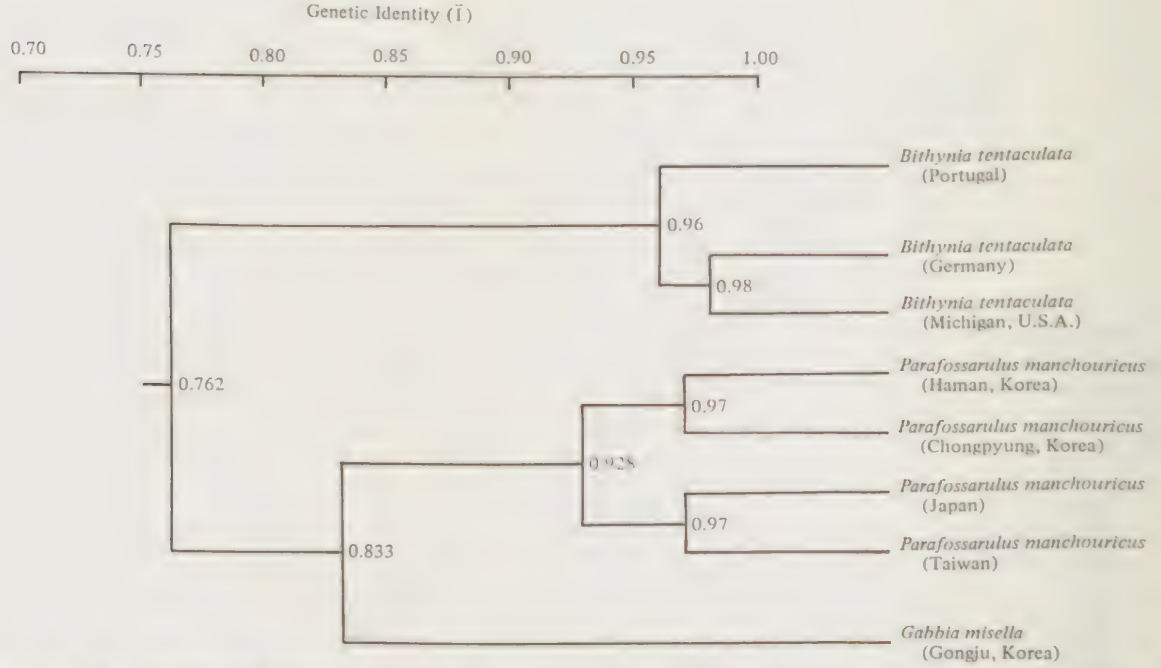

FIG. 66. Phenogram showing genetic relationships based on electrophoretic data of eight populations (three species in three genera) of bithyniid snails.

study. The second group of electromorphs (AcP-2) was polymorphic. The fast band (AcP-2^{104}) was found only in the German and Portuguese strains of *Bithynia tentaculata*, the intermediate band (AcP-2^{102}) was common in all three bithyniid species, and the slow band (AcP-2^{100}) was observed in the populations of *Parafossarulus manchouricus* and *B. tentaculata* (Table 14).

Alanine aminopeptidase [AAP], buffer systems I and II. Buffer systems I and II as applied

in this study were excellent in resolving enzymatic activity of alanine aminopeptidase. Buffer system II was better than I in resolving this enzyme in *Parafossarulus manchouricus*. Monomeric allozyme band patterns were observed in four populations of *P. manchouricus*, and the fast band (AAP^{100}) was common and monomorphic in the populations of *Bithynia tentaculata* and *Gabbia misella* (Table 14).

Leucine aminopeptidase [LAP], buffer systems I, II, III and IV. A single monomorphic band was demonstrated in all bithyniid snails. No intra- and interspecific variation in this enzyme was observed.

Various statistics have been proposed to estimate genetic differences based on polymorphic loci (Cavalli-Sforza, 1969; Hedrick, 1971; Nei, 1972; Rogers, 1972; Richardson & Smouse, 1976; Flake & Lennington, 1977). The most widely used statistical methods are those of Nei (1972). Nei's coefficient of "Genetic identity (I)" ranges from 0 (no alleles in common at a locus) to 1 (the same alleles at identical frequencies). Generally, Nei's coefficient of genetic identity (I) per locus between two taxa is given by

$$I = \frac{\Sigma x_i y_i}{\sqrt{\Sigma x_i^2 \ \Sigma y_i^2}}$$

where x_i and y_i are the frequencies of the ith allele in populations X and Y, respectively. I = 1 when X and Y are monomorphic for the same allele, and I = 0 when X and Y are monomorphic for different alleles. The mean genetic identity ($\bar{I}$) is the mean over-all loci studied (including monomorphic ones) and is most conveniently calculated as

$$\bar{I} = \frac{I_{XY}}{\sqrt{I_X I_Y}}$$

where I_{XY}, I_X and I_Y are the arithmetic means over all loci of $\Sigma\, x_i y_i$, $\Sigma\, x_i^2$ and $\Sigma\, y_i^2$, respectively.

The genetic distance, D, is a measure of genetic differentiation, while heterozygosity, H, is a measure of genetic variation. The genetic distance is simply estimated by

$$D = -\ln I$$

Genetic identity and genetic distance values were calculated for the four allopatric populations of *Parafossarulus manchouricus*, the three populations of *Bithynia tentaculata* and a population of *Gabbia misella* (Table 15). It can be seen that in spite of the great geographical distances between them, the conspecific populations were much more similar to each other than to other species (> 0.90 in genetic identities).

Although a lot of information is contained in a matrix of genetic identity and genetic distance, it is in a form which is difficult to visualize. So, a phenogram was produced on the basis of identity and distance values (Fig. 66). Avise (1974) reported that similarity values between conspecific populations usually fall above 0.85. Data obtained in this study were well matched with Avise's criteria. *Gabbia misella* was genetically closer to *Parafossarulus manchouricus* than to *Bithynia tentaculata*, with 0.83 genetic identity, which is enough to be regarded as different species. The Michigan strain of *B. tentaculata* was genetically closer to the German strain of *B. tentaculata* than to the Portuguese strain, although there was a little genetic difference in terms of genetic identities between taxa. The genetic identity values between conspecific populations generally were high (more than 0.928) in this study.

TABLE 15. Genetic identity ($\bar{I}$) (above diagonal) and genetic distance ($\bar{D}$) (below diagonal) for eight populations of bithyniid snails.

Population*	1	2	3	4	5	6	7	8
1		0.97	0.91	0.96	0.71	0.73	0.71	0.82
2	0.03		0.90	0.94	0.73	0.75	0.74	0.78
3	0.09	0.10		0.97	0.80	0.81	0.79	0.86
4	0.04	0.06	0.03		0.79	0.80	0.77	0.87
5	0.34	0.31	0.22	0.24		0.98	0.96	0.79
6	0.31	0.29	0.21	0.22	0.02		0.96	0.79
7	0.34	0.30	0.24	0.26	0.04	0.04		0.74
8	0.19	0.24	0.15	0.14	0.24	0.24	0.30	

*1, *Parafossarulus manchouricus* (Haman, Korea); 2, *P. manchouricus* (Chongpyung, Korea); 3, *P. manchouricus* (Japan); 4, *P. manchouricus* (Taiwan); 5, *Bithynia tentaculata* (Michigan, U.S.A.); 6, *B. tentaculata* (Germany); 7, *B. tentaculata* (Portugal); 8, *Gabbia misella*.

SDS-polyacrylamide slab gel electrophoresis (Figs. 67-70)

The anionic detergent sodium dodecyl sulfate (SDS) is capable of solubilizing certain classes of proteins, and also of dissociating polymeric molecules into constituent polypeptides. SDS binds to polypeptides and imparts a large negative charge which masks the individual variation in electric charge. So, in SDS-containing gels, polypeptide migration is dependent solely on molecular weight. Thus, it has been proven that SDS gel electrophoresis can be used with great confidence (an accuracy of ± 10%) in determining the molecular weights of polypeptide chains for a wide variety of proteins (Weber & Osborn, 1969).

Figures 67 and 68 show examples of the separation of 26 different polypeptide chains of *Parafossarulus manchouricus*, and Fig. 69 is a comparison of the banding patterns of polypeptide chains in the three bithyniid species employed in this study. Separation of all 26 polypeptide chains was observed without any difference of electrophoretic mobilities of the bands among the three species of bithyniid snails. Fig. 70 is a schematic representation of the results. Four marker proteins, bovine serum albumin, ovalbumin, myoglobin and hemoglobin, were applied in a column of the gel at the same time in order to make a standard curve of their known molecular weights. The molecular weights for the 26 different polypeptide chains of the three species of bithyniid snails ranged from 11,500 to 96,000 (Table 16). (The molecular weight estimates for proteins 1-8 and 24-26 may be less accurate than for proteins 9-23, since the standards did not cover the molecular weights of the two ends of the range.)

Parasitology

Natural infections

Leeches (Annelida: Hirudinea) found in *Parafossarulus manchouricus*. All the leeches found inside or outside the mantles of the *Parafossarulus manchouricus* snails studied here were identified as *Alboglossiphonia heteroclita* (Linnaeus). This species is characterized by its smooth and translucent body and by its three pairs of eyes in an approximately triangular pattern, the first pair always closer to each other than are the two posterior pairs. No leeches were found in *Gabbia misella* from Korea, or in *Bithynia tentaculata* from Hamlin Lake, Michigan, U.S.A.

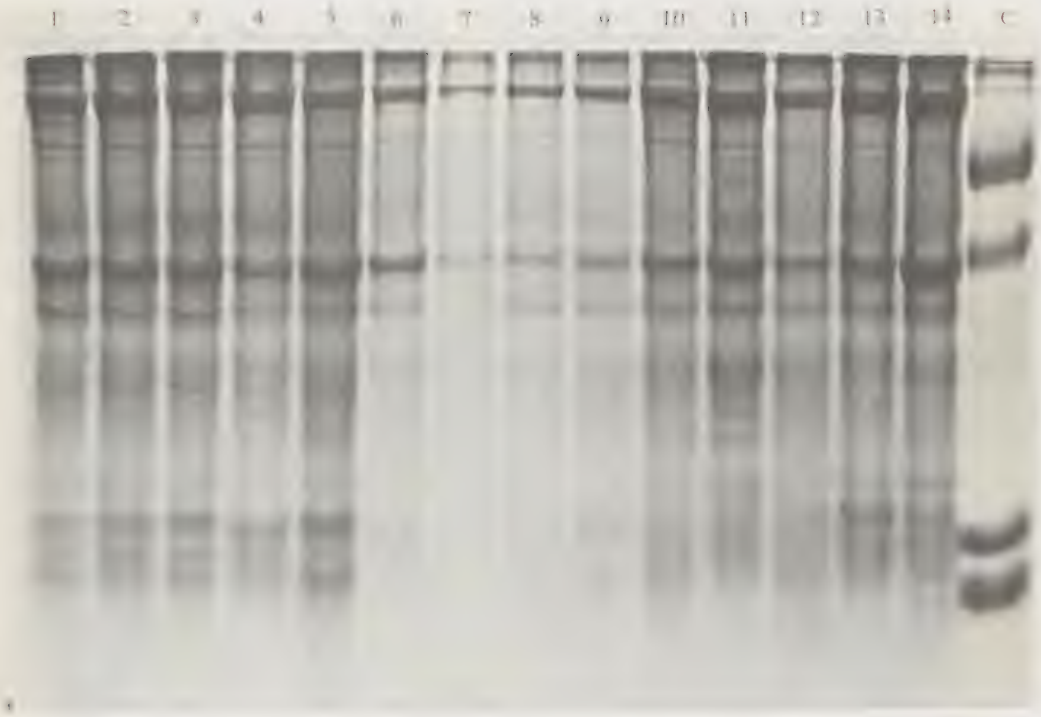

FIG. 67. SDS-PAGE results with *Parafossarulus manchouricus*. 1-3 = Haman population, males; 4-6 = Haman population, females; 7-9 = Chongpyung population, males; 10-12 = Chongpyung population, females; 13 = Japanese strain, male; 14 = Japanese strain, female; C = control (marker proteins).

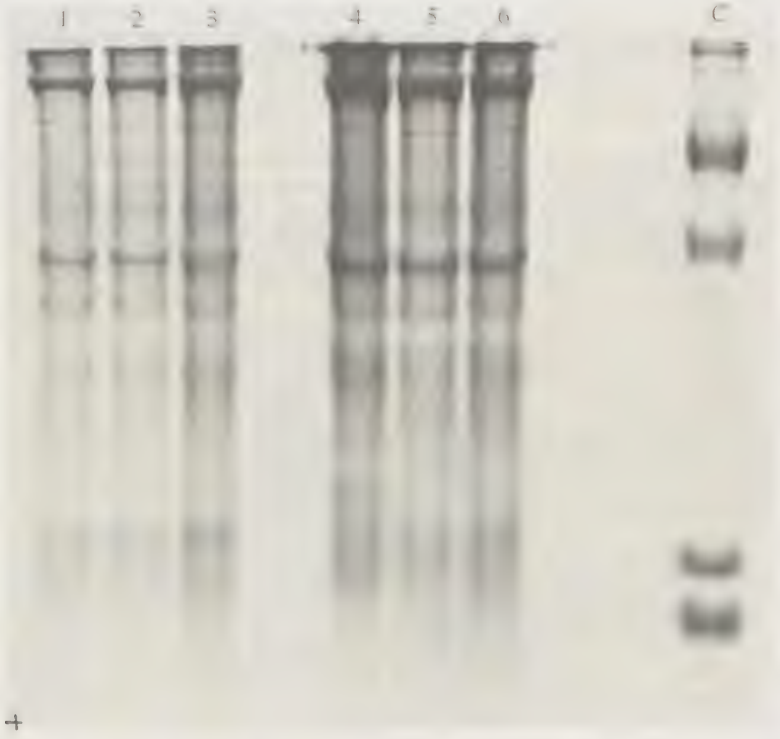

FIG. 68. SDS-PAGE results with *Parafossarulus manchouricus*. 1-3 = Taiwanese strain, males; 4-6 = Taiwanese strain, females; C = control (marker proteins).

FIG. 69. SDS-PAGE results with three species of bithyniids. 1 = *Bithynia tentaculata* (Michigan), male; 2 = *B. tentaculata* (Michigan), female; 3 = *B. tentaculata* (Germany), male; 4 = *B. tentaculata* (Germany), female; 5 = *B. tentaculata* (Portugal), male; 6 = *B. tentaculata* (Portugal), female; 7 = *Parafossarulus manchouricus* (Kwangju), male; 8 = *P. manchouricus* (Kwangju), female; 9 = *Gabbia misella* (Gongju), male; 10 = *G. misella* (Gongju), female; C = control (marker proteins).

FIG. 70. Schematic representation of SDS-PAGE results with bithyniid snails. Twenty-six polypeptide bands were detected in all three species. The marker proteins are shown on the left.

TABLE 16. Electrophoretic mobility and molecular weight of the polypeptide chains in *Parafossarulus manchouricus, Gabbia misella* and *Bithynia tentaculata*.

No. bands*	Distance (mm)†	Mobility‡	Molecular weight
1	1.12	0.01	96,000
2	3.31	0.03	92,000
3	4.39	0.04	90,000
4	6.38	0.06	86,000
5	9.97	0.09	79,500
6	11.08	0.11	76,000
7	12.21	0.12	74,000
8	13.86	0.13	72,000
9	15.81	0.15	68,500
10	18.89	0.18	64,000
11	21.38	0.21	59,500
12	25.15	0.24	54,700
13	27.24	0.26	52,500
14	33.29	0.32	45,500
15	36.67	0.35	42,200
16	39.99	0.38	39,500
17	48.59	0.47	31,800
18	51.67	0.49	30,000
19	55.54	0.53	27,200
20	59.98	0.58	24,100
21	66.37	0.64	20,900
22	72.23	0.69	18,500
23	77.19	0.74	16,300
24	81.11	0.78	14,800
25	85.02	0.82	13,500
26	93.04	0.89	11,500

*The bands were numbered by their migration from their original start to the anodal site in increasing order.

†Total distance of marker dye migration = 104 mm.

‡Mobility = $\frac{\text{distance of protein migration}}{\text{total distance of dye migration.}}$

The infestation rates of the leeches in *Parafossarulus manchouricus* were calculated according to the individual snail populations. Twenty-two out of 167 *P. manchouricus* snails (13.2%) were associated with this glossiphonian leech, although there were variations in the detection rates according to population and to sex (Table 17).

Cercarial trematodes found in natural populations of bithyniid snails. All of the cercariae shed from *Parafossarulus manchouricus* were identified as belonging to the group of pleurolophocercous cercariae, to which the cercariae of *Clonorchis sinensis* belong. These cercariae are characterized by a long tail with caudal finfolds, two eye spots and minute spines on the surface of the body. The oral sucker and pharynx are distinct in this group, but the acetabulum is not fully developed. (Further details of morphological and biological features of these

TABLE 17. Association of leeches with *Parafossarulus manchouricus, Gabbia misella* and *Bithynia tentaculata*.*

Snail species	Snails crushed		Snails with leeches		% infested
P. manchouricus					
Haman strain	Male	90	Male	7	7.8
	Female	13	Female	4	30.8
	Subtotal	103	Subtotal	11	10.7
Kunsan strain	Male	10	Male	2	20.0
	Female	12	Female	3	25.0
	Subtotal	22	Subtotal	5	22.7
Kwangju strain	Male	7	Male	0	0
	Female	8	Female	2	25.0
	Subtotal	15	Subtotal	2	13.3
Chongpyung strain	Male	8	Male	0	0
	Female	4	Female	1	25.0
	Subtotal	12	Subtotal	1	8.3
Kimhae strain	Male	10	Male	1	10.0
	Female	5	Female	2	40.0
	Subtotal	15	Subtotal	3	20.0
	Total	167	Total	22	13.2
G. misella	Male	15	Male	0	0
	Female	40	Female	0	0
	Total	55	Total	0	0
B. tentaculata					
Michigan strain	Male	10	Male	0	0
	Female	10	Female	0	0
	Total	20	Total	0	0
German strain	Total	7	Total	0	0

*All leeches were identified as *Alboglossiphonia heteroclita.*

cercariae have been presented by Muto (1918a, b), Ito (1926), Komiya & Tajimi (1940), Ito (1962) and Chun (1963).) Four out of 103 snails of the Haman strain of *P. manchouricus* (3.88%) shed pleurolophocercous cercariae, and one out of 15 snails (6.66%) collected at Kimhae harbored the cercariae (Table 18). The total infection rate of pleurolophocercous cercariae in *P. manchouricus* was 2.99%. These two areas with infected snails are located along the Nakdong River and are known as high endemic foci of clonorchiasis in Korea. The snails collected at Kunsan, Kwangju and Chongpyung did not release any cercariae.

One out of 55 snails, or 1.82%, of *Gabbia misella* collected in Korea released cercariae belonging to microcercous xiphidiocercaria group (Table 18). These cercariae have a stylet

TABLE 18. Natural infection of *Parafossarulus manchouricus, Gabbia misella* and *Bithynia tentaculata* with trematode cercariae.

Snail species	No. snails examined	No. snails with cercariae	Infection rate (%)
*P. manchouricus**			
Haman strain	103	4	3.88
Kunsan strain	22	0	0
Kwangju strain	15	0	0
Chongpyung strain	12	0	0
Kimhae strain	15	1	6.66
Total	167	5	2.99
G. misella†	55	1	1.82
B. tentaculata			
Michigan strain	20	0	0
German strain	7	0	0
Total	27	0	0

*All of the cercariae shed from *P. manchouricus* were pleurolophocercous cercariae, the group to which *Clonorchis sinensis* cercariae belong.

†One of the 55 *G. misella* snails shed microcercous xipidiocercariae.

at the oral sucker and possess a sharply pointed tail which is shorter than the body. The species of these trematode cercariae were not identified in this study. However, no *G. misella* were found to be harboring pleurolophocercous cercariae.

The *Bithynia tentaculata* employed in this study were not parasitized by any trematodes. However, the sample size of the snails was quite small.

Susceptibility to infection with *Clonorchis sinensis*

Laboratory-bred *Bithynia tentaculata* and *Parafossarulus manchouricus* were used for studying the susceptibility of these snails to infection with *Clonorchis sinensis*. The *Gabbia misella* exposed were uninfected field-collected snails, because not enough laboratory-bred snails were available at the time the susceptibility tests were carried out. Each specimen of the three species of snails was exposed to an average of twelve parasite eggs. An average of ten eggs per snail was eaten by *B. tentaculata*, followed by nine eggs per snail by *P. manchouricus* and six eggs per snail by *G. misella*. Most of the eggs remaining in the vials after the exposure experiment were viable, containing vigorously moving miracidia. No free-swimming miracidia were observed during the experiment.

All of the *Parafossarulus manchouricus* survived during the 12-week observational period after infection (and were still living after 36 weeks), but only 70% of the *Bithynia tentaculata* and 40% of the *Gabbia misella* survived (Table 19). I do not know if any of the *B. tentaculata* or *G. misella* which died were infected with *C. sinensis*. The differences in survival rates might be caused by the ages of the snails and by the sources of the snails used. The specimens of *B. tentaculata* and *P. manchouricus* used were relatively young, 126 and 140

TABLE 19. Survival rates of *Parafossarulus manchouricus, Gabbia misella* and *Bithynia tentaculata* exposed to *Clonorchis sinensis*.

Snail species	Snails exposed*		No. surviving snails (weeks post-exposure)								Total survival rate (%)†
	No.	Age (day)	5	6	7	8	9	10	11	12	
P. manchouricus‡ Kunsan	10 (M)	140	10	10	10	10	10	10	10	10	100
	10 (F)	140	10	10	10	10	10	10	10	10	
G. misella‡	10 (M)	NK	9	8	8	6	6	4	4	4	40
	5 (F)	NK	5	4	4	4	3	3	2	2	
B. tentaculata‡ Michigan	10 (M)	126	7	7	7	7	7	7	6	6	70
	10 (F)	126	8	8	8	8	8	8	8	8	

*Each snail was exposed to 12 eggs of *C. sinensis*.

†Survival rate (%) = $\frac{\text{No. survived}}{\text{No. exposed}}$ x 100.

‡Laboratory bred.

‡Field collected.

Abbreviations: M = male; F = female; NK = not known.

days old, respectively, but the specimens of *G. misella* may have been quite a bit older.

Results of the susceptibility experiments of the three species of bithyniid snails to the Chinese liver fluke *Clonorchis sinensis* are shown in Table 20. The overall infection rates

TABLE 20. Susceptibility of *Parafossarulus manchouricus, Gabbia misella* and *Bithynia tentaculata* to experimental infections with *Clonorchis sinensis*.

Snail species	Snails exposed*		Cumulative no. of positive snails (weeks post-exposure)								Total infection rate (%)†
	No.	Age (day)	5	6	7	8	9	10	11	12	
P. manchouricus‡ Kunsan	10 (M)	140	0	0	0	0	0	0	0	0	15
	10 (F)	140	0	0	0	1	1	2	3	3	
G. misella‡	10 (M)	NK	0	0	0	0	0	0	0	0	0
	5 (F)	NK	0	0	0	0	0	0	0	0	
B. tentaculata‡ Michigan	10 (M)	126	0	0	0	0	0	0	0	0	0
	10 (F)	126	0	0	0	0	0	0	0	0	

*Each snail was exposed to 12 eggs of *C. sinensis*.

†Infection rate (%) = $\frac{\text{No. positive}}{\text{No. exposed}}$ x 100.

‡Laboratory bred.

‡Field collected.

Abbreviations: M = male; F = female; NK = not known.

were 0%, 15.0% and 0% in *Bithynia tentaculata, Parafossarulus manchouricus* and *Gabbia misella*, respectively. The prepatent period of *C. sinensis* in *P. manchouricus* was 8-11 weeks after exposure to the eggs. It is interesting that all of the snails infected were females. None of the field-collected *G. misella* were found to be naturally infected with *Clonorchis* cercariae, and I was not able to experimentally infect any of them. The laboratory-bred *B. tentaculata* also were not susceptible to infection with *Clonorchis*.

DISCUSSION

Culture methods

Successful laboratory culture of any freshwater gastropod is an important first step in pursuing many types of research on such animals, and much effort has been expended on learning how to successfully maintain and culture various freshwater snails, especially those of medical or veterinary importance (e.g., Bruce & Radke, 1971; Liang, 1974; Kitikoon, 1981). Previous to the initiation of my studies, bithyniid snails had not been successfully maintained or cultured in the laboratory, although attempts had been made. Bithyniids were, in fact, considered to be too difficult to raise outside of their natural environment. However, I was successful in the laboratory culture of the species of bithyniid snails I studied, and, during the period of my research, another laboratory (Southeast Asian Center for Applied Malacology, Bangkok) also was successful in culturing their local species of bithyniid snails, *Bithynia siamensis* Lea and *B. funiculata* Walker (Kruatrachue et al., 1982).

Parafossarulus manchouricus is an especially important snail to be able to culture in the laboratory because it is the first intermediate host of *Clonorchis sinensis* and *Echinochasmus perfoliatus* (Ratz) for men and other mammals. To sustain a viable research program on this snail, it is necessary to have sufficient research material. Experimental work with *P. manchouricus* in the past, for example, often has been hampered by the unavailability of material due to inadequate methods of snail culture. Previously, no one had successfully cultured *P. manchouricus, Gabbia misella* and *Bithynia tentaculata* in the laboratory.

For culturing freshwater snails in the laboratory, several factors should be taken into consideration: temperature, light, water quality, population density, type of aquarium, substratum, and parasites and predators. These will be discussed individually below.

Temperature

Many papers have been published in regard to temperature and snail culture, ever since Gordon et al. (1934) reported the optimum temperature for oviposition in *Biomphalaria pfeifferi* (Krauss) and *Bulinus globosus* (Morelet), snail hosts of the parasites causing schistosomiasis (bilharziasis). In the World Health Organization's 1957 report on the ecology of intermediate snail hosts of bilharziasis, the optimum temperatures for the vector snails of human schistosomes were given as being between 22° and 26°C. Bruce & Radke (1971) monitored the daily temperature of snail colonies for the maintenance of *Biomphalaria glabrata* (Say) in the laboratory, and the water temperature of their aquaria was maintained at 26.6°C. Liang (1974) reported that a temperature of 25 ± 3°C represents the optimum temperature for both *Bulinus* and *Biomphalaria* snails. Recently, Chitramvong et al. (1981) reported that the optimum temperatures for the survival of *Bithynia siamensis siamensis* in the laboratory were 20-30°C. The temperatures ranged from 25-27°C throughout my studies.

Light

Boycott (1936) noted that snails were absent from densely shaded ponds and streams. This absence possibly might be related to oxygenation of the water and the production of algae for the snails to eat. Van der Schalie & Davis (1965) raised *Oncomelania hupensis*

formosana (Pilsbry & Hirase) with the highest growth rate under a continuous white, cool fluorescent light. Bruce & Radke (1971) exposed their snail tanks to an alternation of 12 hrs of artificial light (15-watt cool, white fluorescent tubes) and 12 hrs of semidarkness. I followed the methods of Bruce & Radke (1971) and exposed my aquaria to 12 hrs of fluorescent light and 12 hrs of darkness.

Water quality

Bruce & Radke (1971) used warm tap water conditioned before use by filtering it through activated charcoal, and then aerated it for one week prior to use. The pH was regualted to 6.8 (average). Chitramvong et al. (1981) found that salinity and pH values of the water affect the survival of *Bithynia* in the laboratory, the optimum pH values being between pH 6 and 7. Liang (1974) suggested that conditioned water of medium hardness (Ca concentrations of 5 to 40 ppm as $CaCO_3$, and bicarbonate concentrations of 20 to 200 ppm as $CaCO_3$) should be most favorable for culturing snails. In my research program, physicochemical factors of the water, such as salinity and hardness, were not checked. I found that the use of ordinary tap water conditioned with 5% sodium thiosulfate solution, 1N HCl, continuous aeration and maintained at pH 6.5-7.0 provided an excellent medium for snail growth.

Food

Many natural foods (Gordon et al., 1934; Ward et al., 1947; Shah & Gadgil, 1955; Frank, 1963; Chu et al., 1966a,b; Jobin & Michelson, 1967; etc.), synthetic foods (Standen, 1951; Ritchie et al., 1963; Bruce & Radke, 1971; Kruatrachue et al., 1982), and algae (Van Someren, 1946; Gohar & Elgindy, 1962; Kinoti, 1968; Bruce & Radke, 1971; Kitikoon, 1981; Kruatrachue et al., 1982) have been recommended as snail food. However, the recommended quality and quantity of various snail foods differ according to the authors. Tropical fish food ("Tetra SML" flakes), powdered green leaves ("Ceralife") and natural periphyton were used as food for the snails in my study, and these were quite adequate for cultivating the bithyniid snails.

Population density

The stunting of snails due to population density has been observed for many years, ever since Hogg (1854) stated that *Lymnaea stagnalis* (Linnaeus) had the ability of "adapting itself to the necessities of its existence". Liang (1974) recommended using five snails in a commercial plastic tray (7.5 x 20 x 30 cm) for best survival and growth of *Biomphalaria glabrata* and 10 snails per tray for maximum egg production. The 7-liter aquaria that I used in my study each contained fewer than 20 snails and there were no noticeable density effects on snail growth.

Type of aquarium

The different kinds of aquaria used by investigators have been extremely variable, and whether or not the type of aquarium is important in snail culture is not clear. I used conventional glass aquaria, fingerbowls and plastic trays, and since the snails did well in them I did not test the differential applicability of the different types of containers.

Substratum

Various kinds of materials (mud, sand, gravel, clay and various mixtures of these) have been used in attempts to establish favorable substrata for snails (e.g., see Gordon et al., 1934; Chernin, 1957; Liang, 1974). For *Bithynia* cultivation, Kruatrachue et al. (1982) used a thin layer of mud powder. Either mud or sand, or a mixture of both, usually served as satisfactory substratum (Liang, 1974). However, in my study small stones collected for periphyton as a food source of the young snails, rather than mud or sand, served as the substratum.

Parasites and predators

Pringle (1960) found the larvae of four species of chironomid midges invading and destroying the contents of egg masses of *Bulinus globosus* in the laboratory, and Lo (1967) described the deleterious effects of two species of ostracods, *Cypridopsis vidua* (Müller) and *Cypricercus reticulatus* (Zaddach), on snail culture. It is obvious that such harmful co-inhabitants should be eliminated or kept to a minimum in laboratory aquaria.

Of the many factors affecting freshwater snail populations in the laboratory, the presence of suitable foods and stability of the aquarium habitat (Boray, 1964; Eisenberg, 1966) might be the most important for successful cultivation. Nagai et al. (1979) carried out an experimental cultivation of *Semisulcospira libertina* (Gould), the snail intermediate host of *Paragonimus westermani* (Kerbert), with artificial food and using green algae as a habitat stabilizer. Kruatrachue et al. (1982) reared *Bithynia siamensis* and *B. funiculata* using mud as snail substratum and high protein synthetic snail food as the major food source.

Rearing of three bithyniid snails (*Parafossarulus manchouricus*, *Gabbia misella* and *Bithynia tentaculata*) initially was attempted in this study using conventional aquaria. Two generations of the snails have been cultured successfully thus far in this simple system. Fish flakes, "Tetra SML", were sufficient food for the bithyniid snails. However, unconsumed flakes left in the aquarium bottom induced the growth of aquatic bacteria and fungi, which might possibly increase the mortality rate of the snails. Control of the amounts of food and the immediate cleansing of the aquaria which had fungal blooms were necessary for suitable rearing of the bithyniid snails. Powdered green leaves ("Ceralife") and benthic diatoms in the periphyton of the stones are considered as essential food sources, especially for the growing young snails. Further studies on quantitative analysis of the periphyton and the cultivation of the organisms in the laboratory are expected to establish the best methodology and optimum conditions of snail cultivation.

Meier-Brook & Kim (1977) re-confirmed ciliary feeding by bithyniid snails, following the supposition of Starmühlner (1952) and the observations of Schäfer (1952, 1953) that *Bithynia tentaculata* is capable of filter feeding. All three species of bithyniid snails employed in this study were found to be able to filter feed. This mechanism was most readily observed when the snails were fed the powdered Ceralife.

The aquaria were stabilized with aquatic plants such as *Elodea*, *Myriophyllum* and *Sagittaria*, and with small stones encrusted with periphyton. Thick colonies of filamentous algae were occasionally experienced in the aquaria in this study. This growth creates unfavorable conditions for the snails, resulting in inhibition of the usual behavior of the snails and eventually killing them (see also Mori, 1937; Boray, 1964). To prevent the growth of such algae, stones covered with diatoms or green algae (*Myriophyllum* and *Hydrilla*) were put into the aquaria by Nagai et al. (1979). The mortality rate was decreased because of the favorable condition of the habitat. Aquatic plants might be one of the most important factors in stabilizing the habitat (laboratory or natural) of freshwater snails.

Egg-laying characteristics and snail growth

Kruatrachue et al. (1982) reported that approximately two to three weeks after the introduction of adult snails of *Bithynia siamensis* and *B. funiculata* to the breeding cultures, the first eggs were laid on the mud surface or on the sides of the containers. However, they did not mention whether the snails laid their eggs all year round.

The bithyniid snails employed in this study showed a probable trend of biological rhythm in their reproduction. The snails of all three species of bithyniids seem to prefer to lay their eggs once a year, March through June (although there were a few sporadic egg depositions at other times). However, a two or three-year period of observation is necessary to confirm this seasonal rhythm of egg laying.

Vincent et al. (1981) studied the life cycle of *Bithynia tentaculata* over a period of two years in five localities of a freshwater estuary of the St. Lawrence River, Canada. The eggs were laid once a year and growth stopped during winter for about six months. The main phases of individual growth were related to age and thermal variations of the water, and the spawning occurred during the months of May, June and July. This field study on *B. tentaculata* by Vincent et al. (1981) in part supports the present study in terms of egg-laying seasonality of the bithyniids.

The lifespan of *Bithynia tentaculata* was thought to be two to three years by Boycott (1936) and found to be two years by Schäfer (1953). Boycott (1936) used shell growth marks to estimate age, but there are some misgivings about the use of growth marks for determining the age of snails, since such marks may be subject to non-seasonal environmental variation (Hubendick, 1948; Quayle, 1952; Ansell et al., 1964; Craig & Hallam, 1963). It thus would be necessary to check the applicability to the species being considered by experimental marking of individuals or by other means. However, a varix, in general, would seem to be a good indicator of over-wintering. Mattice (1971) confirmed a three-year lifespan in an Oneida Lake population of *B. tentaculata*. Vincent et al. (1981) reported that sexual maturity of *B. tentaculata* inhabiting the St. Lawrence River of Canada is attained after two years and that the species is iteroparous. If the snails lay eggs only once a year (as Vincent et al. (1981) also reported), then those snails have only one chance to lay eggs within their three-year lifespan.

It would seem that the lifespans of the bithyniid snails used in my study might be three years or more, because all three species of field-collected bithyniids are still living in the laboratory after about 17 months, and two massive annual spawnings were observed in the colony of *Parafossarulus manchouricus* (Kimhae, Korea, strain; see Table 4).

Total mortality of field-collected snails of *Parafossarulus manchouricus* was recorded as 31.7% during the 13-month cultivation in this study (Table 6). Nagai et al. (1979) observed that their riverine *Semisulcospira libertina* snails showed high mortality for the first month after the onset of rearing in the laboratory. However, I observed a steady increase in mortality of the bithyniid snails in my studies. This might be related to the characteristics of snails' adaptability to laboratory conditions and the stability of their habitats in the laboratory.

The mortality rate of the young snails of *Parafossarulus manchouricus* was much lower than that of the field-collected snails (4.3% during the 10-month cultivation), although Nagai et al. (1979) reported that the mortality rate of offspring of *Semisulcospira libertina* reached about 85% before shell weight reached 5.0-6.0 mg.

Morphological studies

Shell

Morphological characteristics of the three generic groups studied here are compared in Table 8. Similarities in the shells are: 1) the shells of the three species are all subovately conic, 2) the whorls of the shells of the three species all have distinct transverse growth lines, 3) the sutures of the shells of *Bithynia tentaculata* and *Gabbia misella* are deeply indented, 4) the color of the shells of *Bithynia* and *Gabbia* are deep olive-buff, 5) the opercula of all three species are calcareous and concentric with paucispiral nuclei and 6) the opercula closely fit the peritreme and so are not able to be withdrawn into the aperture of the shells. This is a peculiarity of the Bithyniidae.

The differences between the three species of bithyniid snails employed in this study are: 1) the spirally raised ridges on the whorls of *Parafossarulus manchouricus* against the smooth surface with fine growth lines on the whorls of *Bithynia tentaculata* and *Gabbia misella*, 2) the thickened lips of the apertures of *P. manchouricus* instead of the sharper lips of *B. tentaculata* and *G. misella*, 3) the usually eroded apex in *P. manchouricus*, 4) olive-buff color

of the shells of *P. manchouricus*, 5) well-rounded whorls in *G. misella*, and 6) the size of the shell (the shell length of *G. misella* is not over 7.5 mm, while the shells of the other two species are more than 10 mm in maximum length).

In addition to the above differences, there were some statistical differences among the populations in regard to relative shell heights. Why does morphological variation of the shells take place among the geographical populations? An analysis of shell form in several families of high-intertidal herbivorous gastropods has revealed the existence of morphological gradients (Vermeij, 1973). In Littorinidae, relative spire height and degree of development of external shell sculpture generally increase inter- and intraspecifically, from low to high shore levels. This gradient is also evident from temperate to tropical latitudes. Vermeij (1973) suggested that temperature and desiccation stresses are extremely important physical parameters in the ecological distribution of the species concerned. Certain high-intertidal herbivorous gastropods which potentially can employ evaporative cooling as a mechanism of temperature regulation (Vermeij, 1973), members of the family Planaxidae and the trochid genus *Monodonta*, possess relatively small shell apertures and high spires. This shell morphology is correlated with a fairly high resistance to desiccation. Species of *Monodonta* are known to survive out of water for a period of a week or more (Sourie, 1954; Regis, 1969). In Palau, the very thick-shelled, granularly sculptured *M. labio* (Linnaeus) was found to be one of the most effective temperature regulators studied (Vermeij, 1971). In Hawaii, Struhsaker (1968) found that 28 days of exposure to air were needed to kill 50% of the individuals of the low-spired smooth form of *Nodilittorina picta* (Philippi) which inhabits generally moist surfaces, while 55 days were needed for the higher-spired rough form inhabiting dry surfaces.

Fretter & Graham (1978) are the only other investigators to study the protoconchs of bithyniid snails. They reported that the protoconchs of both *Bithynia tentaculata* and *B. leachi* are "featureless" (although the SEM photographs published by them are not of especially high magnification). In my SEM studies of the protoconch of *Parafossarulus manchouricus*, I found that the sculpture was basically smooth, but on the protoconch there were small, low spiral wrinkles. But, of special significance in Fretter and Graham's observations and my own is that the bithyniid protoconch sculpture is not like that of the Hydrobiidae. The hydrobiids have a distinctly different protoconch sculpture (see Hadžišče et al., 1976; Thompson, 1977, 1979). This sculpture consists of closely spaced, shallow polygonal pits. Therefore, the embryonic shell sculpture is another character differentiating the bithyniids from the hydrobiids.

Radula

Scanning electron microscopy (SEM) of the radulae of the three bithyniid species confirmed the radular formula as 2:1:1:1:2. Morphological differences of the radulae between the populations or species of bithyniid snails are described in detail in the Results section. For example, the central teeth of *Gabbia misella* differ from those of the other species in several respects: 1) the mesocone is larger than the ectocones, 2) there are usually four ectocones on each side of the mesocone, 3) the ridge bearing the basal denticles is more broadly flexed off the lateral margins of the tooth, and 4) the bases of the central teeth are relatively wider.

Walker (1927) reported in his light microscopic study on the radulae of bithyniid snails that radulae of members of the family Bithyniidae are quite similar and do not possess any characters on which generic distinctions can be made. But, as shown in this SEM study, the bithyniid radular morphologies do seem to have some differences even at the species level. More individuals should be studied, since Itagaki (1965) reported that the denticles of the central tooth and the cusps of the teeth of *Parafossarulus manchouricus* are variable in their number between individuals.

Chromosome cytology

The first studies on chromosomes of mollusks date from the late nineteenth and early

twentieth centuries, but the early reports were mostly inaccurate because of inadequate optical equipment and technique (Patterson & Burch, 1978). For example, the paraffin-section technique used in all the early studies compresses the chromosomes, making them smaller (Burch, 1960a). With better equipment and modern techniques, researchers in recent years have accumulated much information on molluscan chromosomes.

In the subclass Streptoneura, chromosome numbers have been determined for species in 23 (19%) out of 121 families. In the large and diverse superfamily Rissooidea (with 18 Recent families), chromosome numbers are known in only three families, the Hydrobiidae, Bithyniidae and Assimineidae. In the family Bithyniidae, the four species investigated previously (*Bithynia tentaculata, B. leachi, B. usseriensis* and *Mysorella costigera*) all have 17 pairs of chromosomes (Butot & Kiauta, 1966; Patterson, 1967) (Table 10).

Von Kemnitz (1914) was the first to produce cytological data on *Bithynia tentaculata*. His chromosomal counts in meiotic divisions of this species, reported as n = 24-28, were incorrect. Ankel (1924) found the haploid chromosome number of *B. tentaculata* to be n=17 and later (Ankel, 1933) gave a good photograph of the chromosomes. This chromosome number was confirmed by Keyl (1955) and Butot & Kiauta (1966), and now by my observations. I also have found that *Parafossarulus manchouricus* has the same number (n=17) as the bithyniids previously studied, but the chromosome number of *Gabbia misella* is n=18.

A general conservativeness with regard to chromosomal change is evident in most molluscan groups (Patterson, 1969). In the Mesogastropoda, all members of the rissooidean families Hydrobiidae and Bithyniidae have 16 to 18 pairs of chromosomes. Results obtained in this study are within this range.

Husted & Burch (1946) pointed out that diploid species can tolerate duplications or addition of chromosomes more easily than loss of chromosomes. Thus, variation in chromosome numbers within a taxon usually reflects addition rather than loss of chromosomes. Burch (1967) followed this hypothesis by giving the lowest number in the range of chromosomal variation as the basic chromosome number for *Semisulcospira* spp. Applying this consideration to my observations, or by simply using the most common chromosome number found in the Bithyniidae, the basic chromosome number for the family would seem to be n=17, 2n= 34. No sex-related, aneuploid or supernumerary chromosomes were found in my studies; all homologous pairs of chromosomes were always well matched.

The karyotype of animals and plants is a species-specific character, and thus it may be helpful to taxonomists studying poorly understood groups. The most extensive comparative karyotype analysis of a snail group has been done by Burch (1967) of the species of the Japanese pleurocerid genus *Semisulcospira*. The systematics of this genus in the Lake Biwa basin was so poorly understood that prior to Burch's study it was not known how many species really existed. Chambers (1982) has recently found karyotypic variation between populations of *Goniobasis* [=*Elimia*] *floridensis* (Reeve) inhabiting different river basins with indistinguishable shell patterns. His observation suggests the parallel evolution of similar shell patterns in populations which have diverged chromosomally. Kitikoon (1982a) observed distinct morphological differences in karyotypes and variation in diploid chromosome numbers in the three "races" of *Tricula aperta* (Temcharoen) he studied. Kitikoon suggested that the "races" he studied actually might be distinct species.

Karyotypic variation between bithyniid species was found in this study, and more interesting was the finding of karyotypic variation in the geographic populations of *Bithynia tentaculata*. As mentioned in the earlier part of this study, some *B. tentaculata* inhabiting the Great Lakes region of the U.S.A. were introduced from Europe long ago by man, while other populations apparently were here before Europeans arrived (Baker, 1928). One pair of metacentric, nine pairs of submetacentric and seven pairs of acrocentric chromosomes were observed in the mitotic metaphase chromosome sets of Michigan *B. tentaculata*, whereas three pairs of metacentrics, 10 pairs of submetacentrics and four pairs of acrocentrics were recognized in

the chromosome sets of the German strain. It is obvious that there has been some chromosomal divergence between these two geographical populations of *B. tentaculata*.

The mitotic and meiotic chromosome cycles have been described in detail for the land snail *Catinella vermeta*, which has only six pairs of chromosomes (Patterson & Burch, 1966). The chromosome cycle in bithyniid snails did not differ from that found in *Catinella* and other animals.

Non-homologous chromosomes do not normally pair during meiosis and hence are usually observed as univalents in meiotic Metaphase I cells (Burch, 1960a, 1967). Such univalents may be sex chromosomes, supernumerary chromosomes or duplications of the normal somatic chromosomes. Burch (1960b) and Patterson (1963) observed heteromorphic chromosomes, presumably related to sex determination, in two species of *Pomatiopsis*, and sex chromosomes were found in the viviparid species *Tulotoma angulata* (Lea) (Patterson, 1965). Kitikoon (1982a) found extra chromosomes in all three races of *Tricula aperta* and thought that they might be sex related. Patterson (1969) concluded that morphologically distinguishable sex chromosomes do exist at least in some bisexual streptoneuran species, even though Nishikawa (1962) stated that sex chromosomes do not exist in prosobranch snails. However, neither univalent chromosomes in meiotic metaphase nor sex chromosomes were found in my study. This does not rule out completely that sex chromosomes do not occur in the Bithyniidae, but, if they do occur, it will take other techniques (such as banding pattern stains) to demonstrate them.

Allozyme electrophoresis

Electrophoresis is the movement of charged molecules in a field of constant direct electric current. All proteins carry an electric charge which is determined by their amino acid composition and the pH of the medium. This charge affects the rate and the direction of movement of molecules in an electric field. Enzymes are structured according to a genetically controlled program and can be separated electrophoretically. Different electrophoretic forms of an enzyme produced by alternative alleles segregating at a locus within a species (allozymes) are the result of genetic variation of these alleles.

There is a general tendency to produce a bias in the estimate of genetic variability when using electrophoretic techniques. Davis (1978) has given several examples of factors producing such bias: two proteins may possibly move with the same electrophoretic mobility in the gel although they have different amino acid sequences; only about 30% of nucleotide substitutions dictate amino acids that effect a net charge in the electrophoretic systems, so that, in these, amino acid changes in a protein may not be detected; genes regulating water-insoluble proteins or membrane-bound proteins will not be detected; and enzymes involved in glucose metabolism are less variable than those acting on substrates such as esters. In spite of these limitations, electrophoresis is a powerful tool and is widely used for biochemical systematics (Davis, 1978).

Electrophoresis was first used on mollusks by Deutsch & McShan (1949) to study land snail blood plasma. Since then, electrophoretic enzyme studies for the detection of allozyme variation among taxa have been employed widely in molluscan systematics (e.g., Wright & Ross, 1963, 1965, 1966; Davis, 1967; Davis & Lindsay, 1967; Burch & Lindsay, 1968; Wu & Burch, 1975; Wurzinger, 1979; Kitikoon, 1982b). Burch & Lindsay (1968) found that the polyploid species of *Bulinus* (e.g. *B. truncatus* species group) were characterized by one particularly dense, fast-moving esterase band, while diploid species, such as *B. tropicus*, had two dense bands. Kitikoon (1982b) observed genotypic differences in the electrophoretically separated isozymes between three races of *Tricula aperta*.

Previous to my studies, bithyniid snails had not been investigated electrophoretically. I used water-soluble enzyme proteins extracted from individual snails to compare genetic variation

among various bithyniid populations. The results showed evidence of genotypic differences between the snail populations (Table 14).

For GOT activity, only a single presumptive genetic locus was observed for all the bithyniid populations (see also Chung & Burch, 1983). The locus contained three presumptive alleles. The fast band (GOT^{103}) occurred only in *Bithynia tentaculata* (monomorphic), although two of 16 Japanese *Parafossarulus manchouricus* had this fast band. The Haman (Korea) and Taiwanese populations of *P. manchouricus* and *Gabbia misella* from Gongju (Korea) had monomorphic medium bands (GOT^{100}), whereas the Chongpyung (Korea) population of *P. manchouricus* showed dimeric medium/slow allelic variation. The Haman area in the southern part of Korea is recognized as one of the high endemic localities of clonorchiasis, and Chongpyung is located just at the border line of low endemic (Goyang Gun, Kyung-Ki Do) and non-endemic (Kangwon Do) localities in the middle part of Korea (Kim, 1974). This raises the question as to whether there is any relationship between allelic variation of the GOT locus in the snails and the endemicity of *Clonorchis sinensis* infection.

It is obvious that there is no gene flow between the Chongpyung and Haman areas from the lack of an allele encoding the slowest GOT band pattern in the Haman population. Why has the Chongpyung population of snails become polymorphic and heterozygous, while all other populations examined exhibited monomorphic or homozygous banding patterns? Does it mean that the high heterozygosity of the GOT locus in the Chongpyung population enables the snails to cope with unfavorable environmental conditions?

Many attempts have been made to relate heterozygosity to environmental variability, although few satisfactory correlations have yet been found (Valentine, 1976). The gene pools in the populations probably vary according to the following causes: age, population size, geographic range, physical environmental stability and tropic resource stability. Each of these factors is discussed below.

Age

Genetic polymorphisms tend to accumulate through time. The older species should be genetically more polymorphic than younger species. Soulé (1972) has proposed that in environments which minimize evolutionary change (e.g., tropical forests, coral reefs and deep-sea environments) the older species should exhibit higher levels of protein polymorphism. A difficulty with this hypothesis is that some very young species are known to display very high genetic variabilities (Valentine, 1976). There is also no evidence that the Chongpyung population of *Parafossarulus manchouricus* is older than the Haman population.

Population size

It might be suggested that variability is correlated directly with population size. Very small populations commonly have little genetic variability. This would be the case under the hypothesis of selective neutrality among polymorphic proteins (Kimura & Ohta, 1971). However, high levels of genetic variability are also found among relatively small populations. It is rather expected that the Chongpyung population might be smaller in size than the Haman population, which has had more chance to spread out due to more stable temperature and habitats. Haman is located in the southern-most part of Korea and at the downstream branches of the River Nakdong, while Chongpyung is located at a higher latitude and in a more mountainous area at the upper portions of the River Han.

Geographic range

A population of the essentially cosmopolitan deep-sea ophiuran *Ophiomusium lymani* Wyville Thomson has no more genetic variability than other deep-sea forms that have far more restricted ranges (Ayala & Valentine, 1974). However, there is no obvious correlation between the extent of species ranges and their genetic variabilities. Japanese and Taiwanese

populations of *Parafossarulus manchouricus* restricted in the islands showed monomorphic single electromorphs of GOT which are exactly matched with the fast band of the Chongpyung population.

Physical environmental stability

Genetic variability should be higher in unstable environments (Levins, 1968). Environmental heterogeneity, temporal or spatial, requires genetic variability to achieve tolerance to changes and to exploit varied opportunities. High frequency of heterozygosity of GOT allozymes in the Chongpyung population of *Parafossarulus manchouricus* may come under this category, because Chongpyung is located at a higher latitude than are the other geographic localities concerned in this study and has a more unstable environment, temporally and spatially. In fact, it can be predicted that the slow bands (GOT^{97}) can be detected in localities at even higher latitudes, such as Siberia and China. But, sometimes this principle is also unpredictable. Gooch & Schopf (1973) first studied deep-sea organisms from the standpoint of their genetic variabilities, and they showed that these organisms do not have particularly low levels as predicted.

Trophic resource stability

There is a clear trend of increasing heterozygosity with increasing benthic ecosystem diversity and presumably with increasing instability of trophic resources (Valentine, 1976). These diversity-correlated trends in genetic variability can be explained in terms of an adaptive-strategy model (Valentine & Ayala, 1974; Ayala et al., 1975a,b). Ayala et al. (1975a) and Valentine & Ayala (1974) hypothesized that, in environments which are temporally coarse-grained for trophic resources (such as high latitudes or regions of highly seasonal or intermittent upwelling), species pursue a relatively fine-grained strategy (such as they would in the tropics and deep sea). In order for a species to perceive a heterogeneous environment as being fine-grained, the species must be flexibly adapted to tolerate a wide range of habitat conditions and to accept a wide variety of food items. Thus, those alleles with products that function in the widest range of conditions are favored by selection; the gene pool therefore comes to consist of only the more flexible alleles.

It would be interesting to determine if a relationship exists between heterozygosity and susceptibility of *Parafossarulus manchouricus* snails to *Clonorchis sinensis* infection. Kitikoon (1982b) reported that the degree of susceptibility to *Schistosoma mekongi* Voge, Bruckner & Bruce may be correlated to GOT mobility. He found that the *Tricula* snails which possessed the fast electromorph (the gamma race) were more susceptible to *S. mekongi* than were the ones that possessed the slow electromorph (the alpha race). Susceptibility tests among the different populations of *P. manchouricus* to *Clonorchis* infection were not performed, although it is known that only *P. manchouricus* is susceptible to *C. sinensis* infection among three species of bithyniid snails employed in the study. Further studies on GOT activity and susceptibility should be undertaken to give a more definite answer regarding possible correlation between the two. In addition to these experiments, it should be determined where the slowest GOT allozyme morphs have originated geographically, and what are the advantageous strategies in the heterozygous populations.

Differences in activity, mobility and number of bands were apparent between individual female and male snails for AlP activity. For AlP-2 and AlP-3, there was no detectable activity for individual males of *Parafossarulus manchouricus*, and no activity at all even in females of *Bithynia tentaculata* and *Gabbia misella*. So AlP-2 and AlP-3 loci are not only sex associated with females but also species specific for *P. manchouricus*. Although the AlP-3 locus expressed monomorphic allozyme bands in the females of *P. manchouricus*, the AlP-2 locus showed dimeric, polymorphic allozyme morphs in the females of the Korean, Japanese and Taiwanese populations. That is, Korean (Haman and Chongpyung) strains of female *P.*

manchouricus had only the fast band (AlP-2^{100}) and the Japanese strain showed only the slow band (AlP-2^{98}). But, the Taiwanese females expressed both of the alleles, showing dimeric heterozygous banding patterns. In addition to the fact that the AlP-2 locus in *P. manchouricus* is associated with only females, this locus enables a hypothesis regarding the zoogeographic origin of *P. manchouricus* in Taiwan: they are mixtures of snails originating from both Korea and Japan.

Proteins which are limited to one sex have been found occasionally, e.g., a kidney esterase in mice (Shaw & Koen, 1963) and an amylase in *Drosophila hydei* Sturtevant (Doane et al., 1975). There are a number of sex-limited proteins restricted to the gonads (Ferguson, 1980). Also, the gene encoding enzymes such as glucose-6-phosphate dehydrogenase and phosphoglycerate kinase in man and kangaroo (Cooper et al., 1975) are on the X chromosome. It is unknown whether AlP-2 and AlP-3 loci in the females of *Parafossarulus manchouricus* are associated with sexual organs or sex chromosomes.

Five isozyme bands of esterase were detected electrophoretically. EST-1, EST-2 and EST-3 loci were common in all the bithyniid populations in this study. In regard to EST-4 activity, the fast band (EST-4^{104}) was found only in the Portuguese population of *Bithynia tentaculata* and showed a monomeric combination with the slow bands (EST-4^{100}), which appeared in all the populations of *B. tentaculata*.

Avise (1974) suggested that if similarities between populations are arranged on a scale from 0 to 1, with 1 indicating genetic identity, conspecific populations usually fall above 0.85. As shown in a phenogram in this study (Fig. 66), the Michigan strain of *Bithynia tentaculata* is genetically closer to the German strain (I = 0.98) than to the Portuguese strain (I = 0.96), and the *Gabbia misella* snails are closer to the *Parafossarulus manchouricus* group (I = 0.833) than to the populations of *B. tentaculata* (I = 0.762). This would seem to indicate that *G. misella* either should stand alone as a genus or should be included as a subgenus of *Parafossarulus* (rather than as a subgenus of *Bithynia* as it is frequently placed).

AlP-1, AcP-2 and AAP loci showed allelic variation between the populations of the same species or between the three bithyniid species.

There appears to be some difference between species in α-glycerophosphate dehydrogenase, in that it was detected in *Bithynia tentaculata*, but not in *Gabbia misella* and *Parafossarulus manchouricus*. Why this dehydrogenase was not detected in the latter two species is not known. Perhaps they occurred in amounts below the resolution of my techniques.

SDS-PAGE electrophoresis

Sodium-dodecyl sulfate polyacrylamide slab gel electrophoresis (SDS-PAGE) was applied in this study in order to compare molecular variation among the bithyniid species. However, since no variation was seen between any of the populations or species, this method does not seem to be applicable to studying individuals at the population and lower taxonomic levels (e.g., species or subspecies), although it possibly may prove to be of value in studying higher taxa. (Two dimensional SDS-PAGE may be useful for studying protein variations between the lower taxonomic levels.)

Parasitology

Natural infections

Aquatic leeches are usually predators or parasites, and some have medical importance in that they serve as the first and second intermediate hosts, or as final hosts, of parasitic protozoans, trematodes, cestodes, nematodes and nematomorphs (Klemm, 1976). The most important environmental factor influencing the abundance and distribution of freshwater leeches is the availability of food organisms (Sawyer, 1974; Klemm, 1976). Most parasitic

leeches are not host specific, but they tend to restrict their diets to certain groups of animals. In the United States and Canada, there are about 51 species of freshwater leeches belonging to the four major families of the Hirudinea: Glossiphoniidae, Piscicolidae, Erpobdellidae and Hirudinidae (Sawyer, 1974). Among those, eleven species are reported living in North American snails and clams (Klemm, 1976). Moore (1939) reported that most of the smaller species of Glossiphoniidae are habitually malacophagous and that they feed almost exclusively on aquatic snails. Snail-associated genera of the Glossiphoniidae are *Glossiphonia*, most *Helobdella* and *Marvinmeyeria*. Klemm (1976) reported that three species of *Glossiphonia*, five species of *Helobdella* and one species of *Marvinmeyeria* were associated with North American snails. Besides the so-called snail-leeches, *Batracobdella* sp. feed on amphibians, *Placobdella* on turtles, *Theromyzon* on aquatic birds, piscicolid leeches on fish, and erpobdellid leeches feed on aquatic insect larvae and oligochaetes (Sawyer, 1974).

No previous report on the Korean leech fauna of snails is known to me. No leeches were detected infesting *Gabbia misella*, but *Alboglossiphonia heteroclita* was found on Korean *Parafossarulus manchouricus*. *A. heteroclita* has a wide distribution, although it is considered to be rare, at least in North America (Klemm, 1972a; Sawyer, 1972; Davies, 1973), but probably it is frequently overlooked because of its small size and inconspicuous coloration (Klemm, 1976). In Europe, *A. heteroclita* inhabits the mantle cavity of freshwater snails (mainly *Radix pereger* (Müller)) from October to May, with a peak infestation in January (Gruffydd, 1965; Hatto, 1968). During their breeding season, from May to October, they are free living. Klemm (1976) listed 14 snail species, including *Bithynia tentaculata*, as hosts of *A. heteroclita* in the Holarctic region (Europe and North America), India, and Central and East Africa. This leech species appears sensitive to prolonged high temperatures (Sawyer, 1974).

More extensive studies on Korean leeches and snails, and on their inter-relationships, should be undertaken. Further studies are needed to know whether or not there is any preference of the leeches in selecting their hosts, and, if there is, is this selection species specific. Also, it would be important to know if leeches have any deleterious effects on *Parafossarulus manchouricus* and, if so, how the leeches might be used in controlling these intermediate host snails.

Also, attention should be directed to possible associations of other annelid worms with snails. For example, I usually observed *Chaetogaster* sp. (Oligochaeta, Aeolosomatidae) associated with the egg masses of *Parafossarulus manchouricus* during laboratory cultivation in finger bowls, but whether or not the annelids had a deleterious effect on the eggs was not studied.

Parafossarulus manchouricus is the intermediate host of *Clonorchis sinensis* in the Orient, and of *Echinochasmus perfoliatus* (an occasional echinostome of man) as well (Malek, 1962). *Bithynia tentaculata* is the intermediate host of several trematodes, e.g., the psilostome *Psilotrema spiculigerum* (Mühl) and the strigeid *Apatemon gracilis* (Rudolphi), both of which infect ducks. No human trematode parasites are known to infect *B. tentaculata* (Malek, 1962) and, as far as I know, no trematodes at all have been reported to infect *Gabbia misella*.

In my study, a total of 249 bithyniid snails were crushed to search for trematode cercariae. All the cercariae shed from *Parafossarulus manchouricus* were identified as pleurolophocerca, a group to which *Clonorchis sinensis* cercariae belong. The infection rate of the snails having these cercariae was low (2.99%), similar to that found by Kim (1974) (2.3-3.1%) for *C. sinensis* in Korea in both high and low endemic localities.

Cercarial liberation from snails occurs in nature in the period from May to October in Korea. During the cooler season, the rest of the year, the cercariae do not appear. *Clonorchis* cercariae in the snail exposed to low temperature (4°C) lose viability within several days (Kim, 1974). Kim (1974) also found much fatal damage by rediae to snails collected from the field in winter and suggested that the snails acquire a new infection each year in early spring. The snails employed in this study were all collected in summer and examined at room temperature.

Susceptibility of bithyniid snails to *Clonorchis sinensis*

Clonorchiasis has been known to be endemic to the Orient for the past hundred years, and this disease has been recognized to be closely related to the distribution of the snail intermediate hosts since 1918, when Muto (1918a,b) found a freshwater bithyniid snail, *Parafossarulus manchouricus*, to be the fluke's first intermediate host. In Korea, Shiba (1933) found two species of bithyniid snail, *Bulimus striatus* Benson (= *P. manchouricus*) and *B. kiusiuensis* Hirase (= *Gabbia misella*), and reported that *B. striatus* probably would serve as the first intermediate host of *Clonorchis sinensis*, but whether or not *B. kiusiuensis* also could serve as a host was not known. Soh (1978) suggested the possibility that *G. misella* might serve as the snail intermediate host of *C. sinensis*. Little has been known about the details of susceptibility of bithyniid snails, although Higuchi (1938) observed that it took 26 days for *Clonorchis* miracidia to develop to cercariae in the snail host after infection. But, Higuchi employed field-collected *P. manchouricus*. The main reason that it has been difficult previously to study susceptibility in bithyniid snails has been due to the lack of laboratory culturing techniques.

Faust & Khaw (1927) studied the hatching of *Clonorchis* eggs. They found that, although eggs contain fully developed and mature embryos at the time of discharge from the worm, they do not hatch, but degenerate unless certain factors come into operation. Under experimental conditions, these factors were 1) abrupt change of temperature, 2) alternate freezing and thawing, 3) mechanical pressure or impact and 4) temporary alteration of the tonicity of the medium. They considered that there are two methods potentially available for the miracidium of *Clonorchis* to enter the mollusk. The first is that the mature miracidium hatches out due to the popping off of the operculum of the egg shell, swims about in the surrounding medium, comes within the immediate vicinity of the appropriate species of snail, and penetrates the tissue of the snail. The alternative method is for the snails to ingest the miracidia, either unhatched or hatched. This second possibility is strongly supported by my studies. No free-swimming miracidia were observed in my experiment, in spite of the fact that all eggs were in water for 17 hrs while the snails were being exposed to them.

Nagano (1926) placed 20 young (presumably uninfected) snails of *Parafossarulus striatulus* var. *japonicus* (Pilsbry) (= *P. manchouricus*) in tap water for 10 days, after which he placed *Clonorchis* eggs in the container. He found a sporocyst and some small active rediae along the wall of the intestine of four of the snails on the 29th day after exposure to the eggs. Nagano believed "that the egg is first passively taken in by the snail, and then its further development takes place". Higuchi (1938) observed that it took 26 days for *Clonorchis* miracidia to develop to cercariae in the snail host after infection.

Faust & Khaw (1927) reported experimental results on the viability of *Clonorchis* eggs in the snails. In several individuals of *Parafossarulus manchouricus* dissected five weeks after infection, there were still a number of unhatched viable ova in the gut, indicating that a portion of the ova may remain in the gut of the snail for at least five weeks without undergoing degeneration. This fact may explain why *P. manchouricus* snails infected with *Clonorchis* eggs released *Clonorchis* cercariae so late (8 to 11 weeks post-infection in my study), in contrast to the data of Nagano (1926) and Higuchi (1938). However, the overall infection rate of the snail with *C. sinensis* in my experiment generally agreed with Nagano's data.

On the resumption of cercarial emergence from the snail following hibernation in spring, Inatomi (1953), in his study conducted in Okayama, Japan, presumed that the *Clonorchis* miracidia that penetrated the snail before hibernation spent the winter period in the liver of the snail in a redial state, becoming cercariae and being liberated around April, at the time that the snail resumed its spring activity. However, Kim (1974) disagreed with this. He explained that *Clonorchis* cercariae in the snail lose their viability within several days when the snail is exposed to low temperature (4°C). Mature rediae of *Clonorchis* were also seriously affected, under the same temperature, losing viability. He presumed that it is probable in

such a cold climate as Korea's that the snails acquire a new infection each year and release cercariae about the month of May. However, the possibility of the survival during the winter of immature *Clonorchis* larvae (e.g., sporocysts) is not completely eliminated, because of the long prepatent period of *C. sinensis* in the snails as shown in this experiment (8-11 weeks) (although my experiment was carried out under laboratory conditions and with laboratory-bred snails).

Ever since Muto discovered that the first intermediate host of *Clonorchis sinensis* in Japan was *Parafossarulus manchouricus*, many investigations dealing with the infection of *P. manchouricus* with cercariae of *C. sinensis* have been made in Korea (Kobayashi, 1922; Shiba, 1933; Nishimura, 1943; Lee & Kim, 1958; Choi et al., 1975; Chun, 1963; Chung et al., 1980). However, those investigations were carried out with field-collected specimens only, so that natural infection of various trematode cercariae (including *C. sinensis*) in the snails must be taken into consideration.

In my experiment, all of the *Parafossarulus manchouricus* snails were laboratory bred and free from any trematode parasites before setting up the susceptibility studies. My studies are the first time that susceptibility data from laboratory-bred snail hosts of *Clonorchis sinensis* have been obtained. Even though the infection rate in the snails was quite low, the three snails that were infected were still producing cercariae as late as 24 weeks post-patency. Due to this long period of time, and since I also found in my experiment that each snail could shed as many as 25 cercariae per hour, it can be seen that only a few positive snails at a transmission site are enough to keep the trematode's life cycle going.

SUMMARY

Seven different populations of *Parafossarulus manchouricus* (Kimhae, Kunsan, Kwangju, Chongpyung and Haman, Korea; Kurume, Japan; and Taipei, Taiwan), a population of *Gabbia misella* (Gongju, Korea) and three different populations of *Bithynia tentaculata* (Michigan, U.S.A.; Bodensee, Germany; and southern Portugal) were compared in regard to egg-laying characteristics, morphology, chromosome cytology, allozyme electrophoresis and natural infections of parasites and susceptibility to infection with *Clonorchis sinensis*.

A satisfactory culture method was devised for laboratory rearing of the snails. Tropical fish food (Tetra SML) and powdered green leaves (Ceralife) were used as the main food sources for the snails. Benthic diatoms such as *Navicula* and *Gomphonema* from the periphyton also were used, and they seemed essential for satisfactory growth of baby snails. The powdered leaves were ingested by ciliary filter feeding. The aquaria were stabilized with small stones from a local stream and with aquatic plants (*Elodea, Myriophyllum* and *Sagittaria*). Young *Parafossarulus manchouricus* snails grew to adult size in about 54 days after hatching. They laid eggs 150-156 days after hatching. The whole cycle (birth to egg laying) took approximately five months. The three species of bithyniid snails are iteroparous and lay eggs once a year.

There were no major morphological differences in the shells of the genera studied here. The following rather minor differences were observed in the shells. The shell of *Parafossarulus* has spirally raised ridges, and its apex is usually eroded; the other two genera lack these characteristics. The shell of *Gabbia misella* is small, not exceeding 7.5 mm in length, while the shells of the other two species are larger, being more than 10 mm in length. There were some statistical differences in shell heights between the Korean and the other populations of *P. manchouricus*, and between this species and the other two bithyniids as well. The shell differences between the several populations of Korean *P. manchouricus* may be related to environment.

Scanning electron microscopy (SEM) of the protoconch of *Parafossarulus manchouricus* reveals nearly smooth sculpture with small, low, spiral wrinkles. This sculpture is quite different from that of the Hydrobiidae, a family to which the bithyniids are frequently assigned.

Scanning electron microscopy of the radulae of the three bithyniid species showed that their radular morphologies are very similar, but there are some small differences, which may be species specific.

Details of the chromosome cycle of these bithyniid snails are similar to those reported for other snails, and no specific differences were observed in the chromosome cycle between the three species of snails employed in this study. Two different chromosome numbers were observed in the three bithyniid species: n=17 in *Parafossarulus manchouricus* and *Bithynia tentaculata*, and n=18 in *Gabbia misella*. No sex chromosomes or supernumerary chromosomes were seen. There were morphological differences in the karyotypes of the three species. Additionally, the European and American strains of *B. tentaculata* were observed to have karyotypic differences: the Michigan strain had one metacentric, nine submetacentric and seven acrocentric chromosome pairs, while the German strain had three metacentric pairs, 10 submetacentrics and four acrocentrics. These differences probably have resulted from the long separation of the populations on the two continents.

Allozyme variations between the allopatric populations of *Parafossarulus manchouricus*, *Gabbia misella* and *Bithynia tentaculata* were observed in GOT, AlP-1, AlP-2, AlP-3, AcP-2, AAP, EST-4 and EST-5 activities. In the Chongpyung, Korea, population of *P. manchouricus*, some individuals had a unique GOT electromorph (slow bands) which was not detected in the other populations (even in the Haman, Korea, population), and which showed typical dimeric banding patterns. Actually, the mobility of the electromorphs of *G. misella* was identical with the fast bands of *P. manchouricus*; however, the monomorphic single-banded morphs of *B. tentaculata* populations migrated faster than the fast bands of *P. manchouricus* and *G. misella*. So, the fastest morphs for GOT activity were species specific for *B. tentaculata*, and the slow bands were specific for the Chongpyung, Korea, population of *P. manchouricus*, where they may be related to nonsusceptibility to *Clonorchis* infection.

The fast bands for EST-4 activity were population specific for the Portuguese strain of *Bithynia tentaculata*, the medium bands for the German strain of *B. tentaculata*, and the slow bands were common to all the bithyniid species.

The allozymes encoded by AlP-2 and AlP-3 loci were all associated with the female snails, and were found only in the populations of *Parafossarulus manchouricus*. The fast band for AlP-2 activity was seen only in Korean populations (Haman and Chongpyung) of *P. manchouricus*, while the slow band was detectable only in the Japanese population of *P. manchouricus*. Heterozygous banding patterns of the above-mentioned homozygotes (fast and slow bands) occurred only in the Taiwanese population of *P. manchouricus*. These sex-related allozyme patterns seem to suggest a hybrid origin (from Korean and Japanese snails) for the Taiwanese population. For AlP-3 activity in *P. manchouricus*, the enzyme proteins all migrated cathodally and were monomorphic in all the females.

Although sodium dodecyl sulfate-polyacrylamide slab gel electrophoresis (SDS-PAGE) provided separation of 26 polypeptide chains, there were no distinct differences in electrophoretic mobilities of the bands among the three bithyniid species. The molecular weights for 26 different polypeptide chains of the three species ranged from 11,500 to 96,000.

The freshwater leech *Alboglossiphonia heteroclita* was found inside and outside the mantles of the *Parafossarulus manchouricus* snails, but no leeches were found in *Gabbia misella* from Korea or in *Bithynia tentaculata* from Michigan, U.S.A. The infestation rates of the leeches in *P. manchouricus* was 13.2%.

The total infection rate of pleurolophocercous cercariae in field-collected *Parafossarulus manchouricus* was 2.99%. No pleurolophocercous cercariae were shed from the other two bithyniid species.

Susceptibility of *Parafossarulus manchouricus* (Kunsan, Korea, strain), *Gabbia misella* (Gongju, Korea) and *Bithynia tentaculata* (Michigan, U.S.A.) to infection with *Clonorchis sinensis* was studied. The laboratory-bred *P. manchouricus* were susceptible to *C. sinensis*,

with an overall infection rate of 15%. However, laboratory-bred *B. tentaculata* and field-collected *G. misella* were completely nonsusceptible to *C. sinensis*. Therefore, in Korea, *G. misella* need not be emphasized in clonorchiasis surveys.

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THE RADULAR TEETH OF SELECTED PLANORBIDAE[1]

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ABSTRACT

The radular teeth of various of the Planorbidae studied show certain common distinctive characteristics. The majority of the species have bilaterally symmetrical bicuspid central teeth, tricuspid lateral teeth and rake-like (comb-like) marginal teeth. However, three of the small Australian species, *"Isidorella" sisurnia, Camptoceras cosmeta* and *Bayardella johni*, have asymmetrical cusp development of the central teeth, in which one of the main cusps is noticeably larger than its counterpart. A continuation of this asymmetrical development probably produced the five-cusped central tooth of the Neotropical *Plesiophysa*. The lateral teeth of *C. cosmeta* and *B. johni* also differ from the other planorbids studied by the reduction of the entocone and the early division of the ectocone into cusps. The lateral teeth of *B. johni* are the most extreme in this regard, possessing an enormous mesocone, reduction of the endocone and the separation of the multicuspid ectocones from the mesocone-ectocone subunit near the hook-body.

The most distinctive teeth of the snails studied belong to *Gyraulus essingtonensis*; their basic cusp structure, for the central and lateral/marginal teeth alike, is unlike that of the other planorbids. These differences have been reported previously, but the SEM corroborates and emphasizes them.

Speculation about the phylogenetic significance of the radular tooth differences in the Planorbidae should await details about the food and feeding habitats of these snails.

INTRODUCTION

The Planorbidae are a family of freshwater pulmonate gastropods with world-wide distribution. They are among the most diverse of all the freshwater snails, and as a group they are the most medically important. Because of their significance to human health, several of the genera have received considerable attention. Other genera have been studied very little. There are few adequate taxonomic studies on the family at the species level. F.C. Baker had embarked on such a study, but unfortunately he did not live to see his monograph completed. The posthumous publication of Baker's manuscript (Baker, 1945), assembled from Baker's notes by Harley J. Van Cleave, is incomplete in many details, as might be expected. It is especially inadequate in dealing with species-level taxonomy and with intergeneric relationships.

Hubendick (1955) published a comparative anatomical study of representatives of most of the various planorbid generic groups, and indicated certain possible or probable phylogenetic relationships within the family. It is unfortunate that Hubendick's anatomical-phylogenetic studies have not been followed, except for several species, by more detailed and more comprehensive investigations.

Hubendick (1955) observed that the planorbids he had studied fell into three groups on the basis of radular tooth characteristics. One of the radular groups corresponded to his monogeneric subfamily Plesiophysinae. Here the main distinction was the "three well-developed cusps on the centrals." The second radular type "characterizes all the Bulininae as well as several groups of Planorbinae", by possessing . . . "long, oblique type of marginals with cusps not only on the posterior end of the tooth but also along its lateral margin". The third

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radular type "has shorter [marginals], comparatively symmetrical and without cusps along the lateral edge. The latter occurs exclusively in the Planorbinae". This third group comprises the *Acrorbis, Planorbis* and *Segmentina* tribes.

The purpose of the present study was to investigate the radular characters of various selected Planorbidae with the scanning electron microscope (SEM), and to compare our observations with Hubendick's radular groups. The SEM gives a much clearer picture of radular tooth detail than does the light microscope. Included in our study are several generic groups (*Bayardella, Helisoma* s.s. and *Isidorella*) not observed by Hubendick.

MATERIALS AND METHODS

The snails used in this study are listed below. The species are listed alphabetically in the three subfamilies recognized by Hubendick (1955). Nearly all of the snails were collected by J.B. Burch, accompanied by various colleagues or assistants. SEM observations were made on two specimens of each species, except for the Australian species, of which three specimens were used. These studies were supplemented by observations on the radulae of additional specimens with a light microscope. The radular teeth descriptions which follow are from one selected individual of each species. Duplicate specimens are in The University of Michigan Museum of Zoology, the Australian Museum and Yonsei University, Seoul.

Subfamily Bulininae

Bulinus tropicus (Krauss) (Fig. 1a). Laboratory stock from South Africa in aquaria in the Museum of Zoology, The University of Michigan, Ann Arbor, Michigan, U.S.A.

Bulinus truncatus (Audouin) (Fig. 1b). Laboratory stock from the Sudan in aquaria in the Museum of Zoology, The University of Michigan, Ann Arbor, Michigan, U.S.A.

Subfamily Planorbinae

Amerianna carinata compar Iredale (Fig. 1h). Pond near the entrance of Hidden Valley, just outside of Kununurra, Western Australia, Australia.

Camptoceras cosmeta (Iredale) (Fig. 1j). Roadside ditch on road between Grong Grong and Coolamon, three miles west of Ganmain, New South Wales, Australia.

Gyraulus essingtonensis (Smith) (Fig. 1l). Bow River, Great Northern Highway, Western Australia, Australia.

Helisoma anceps (Menke) (Fig. 1g). Fleming Creek, The University of Michigan Botanical Garden, near Ann Arbor, Michigan, U.S.A.

Isidorella newcombi (Adams & Angas) (Fig. 1c). Swamp at turnoff to Four Corners on Newell Highway (Highway 39), six km southwest of Morundah, New South Wales, Australia.

Isidorella newcombi (Adams & Angas) (Fig. 1d). Spencer's Gorge, Macdonnell Ranges, Northern Territory, Australia.

"Isidorella" sisurnia (Hedley) (Fig. 1i). Pond near entrance of Hidden Valley, just outside of Kununurra, Western Australia, Australia.

Physastra concinna (Adams & Angas) (Fig. 1e). Billabong near King River, Northern Territory, Australia.

Planorbella trivolvis (Say) (Fig. 1f). Lake shore of Lake Huron, Mackinac City, Michigan, U.S.A.

Subfamily Plesiophysinae (?)

Bayardella johni (Burch) (Fig. 1k). Bow River, Great Northern Highway, Western Australia, Australia.

Radula preparation for SEM observation

The tissues of the buccal masses of the snails were partially dissolved in 10% potassium hydroxide (KOH) solution to facilitate separation of the radular ribbon. This process took 7-24 hr at room temperature or 5-20 min in an incubator at 60°C. While in the KOH, the buccal masses of juvenile animals had to be checked very often in order to prevent dissolution of the radular ribbon. The radulae, easily dissected from the disintegrating muscle tissues and adherent membranes of the macerated buccal masses, were transferred to vials containing 70% ethanol for storage.

To clean the radulae after removal from the buccal masses, the specimen vials were partly immersed into the tank of an ultrasonic cleaner and sonicated for 5-15 sec. The sonicated ethanol containing the radulae was drained and replaced with fresh 70% ethanol. If the ethanol solution showed precipitated materials, then one or two more ethanol washes or sonications were performed.

The SEM stub, well cleaned with ethanol and wiped dry with a lint-free tissue, was covered with double-sided clear tape, and aluminum paint was applied on the transition from tape to stub to insure the conduction of current from the specimen to the stub.

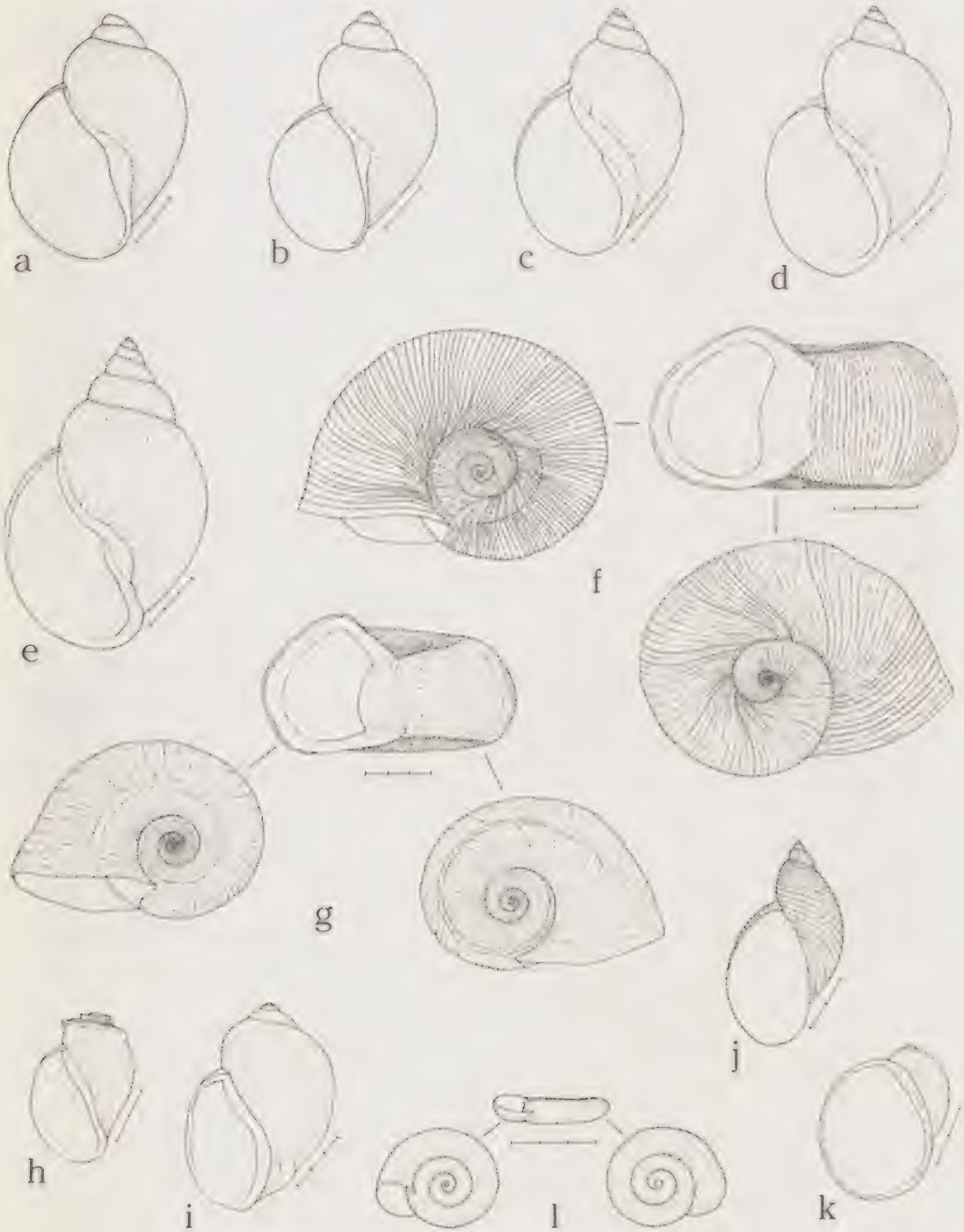


FIG. 1. Shells of the planorbid species used in this study. a, *Bulinus tropicus*; b, *B. truncatus*; c, *Isidorella newcombi* (nr. Morundah); d, *I. newcombi* (Spencer's Gorge); e, *Physastra concinna*; f, *Planorbella trivolvis*; g, *Helisoma anceps*; h, *Amerianna carinata compar*; i, *"Isidorella" sisurnia*; j, *Camptoceras cosmeta*; k, *Bayardella johni*; l, *Gyraulus essingtonensis*. Measurement lines = mm.

The radula which had already been cleaned and preserved in 70% ethanol was transferred to a Stender dish containing double distilled water to remove the alcohol from the radula. Then, by using a dropping pipette, the radula was placed on a depression slide with distilled water and studied under the light microscope to determine the orientation of the radular ribbon.

The stub was covered with a drop of double-distilled water and the radula was transferred from the slide to the stub with the dropping pipette. Under the dissecting microscope, the radula was spread easily with the help of microdissection forceps and a fine brush.

When the radula was well positioned on the stub, the excess water was removed with a brush or a capillary dropper and the remaining water was allowed to evaporate completely in the open air at room temperature on in an incubator at 37°C. (Radulae which were dehydrated in a graded series of alcohol concentrations became unmanageable because of hardness. Also, when a drop of 70% ethanol was placed on the tape attached to the top of the SEM stub in order to position the radulae, it was difficult to handle the radulae because the alcohol partially dissolved the glue of the tape. For these reasons, the radulae were not dehydrated before setting them on the tape, but fixed and washed with 70% ethanol and transferred to water so as to spread them on the tape.)

In order to observe the radulae from various angles, one or two short copper wires were placed on the tape and their two ends were glued to the stub with aluminum paint before placing the radulae on the tape. The diameters of the wires used for this purpose were various (0.2-2.0 mm), depending on the radulae sizes and desired viewing angles. The radulae were placed on the wires perpendicular to the longitudinal axis of the wire or in other directions as desired.

The completely dried radulae were stored in dust-free containers until the gold coating was applied and the radulae were observed with the SEM (JEOL JSM-U3).

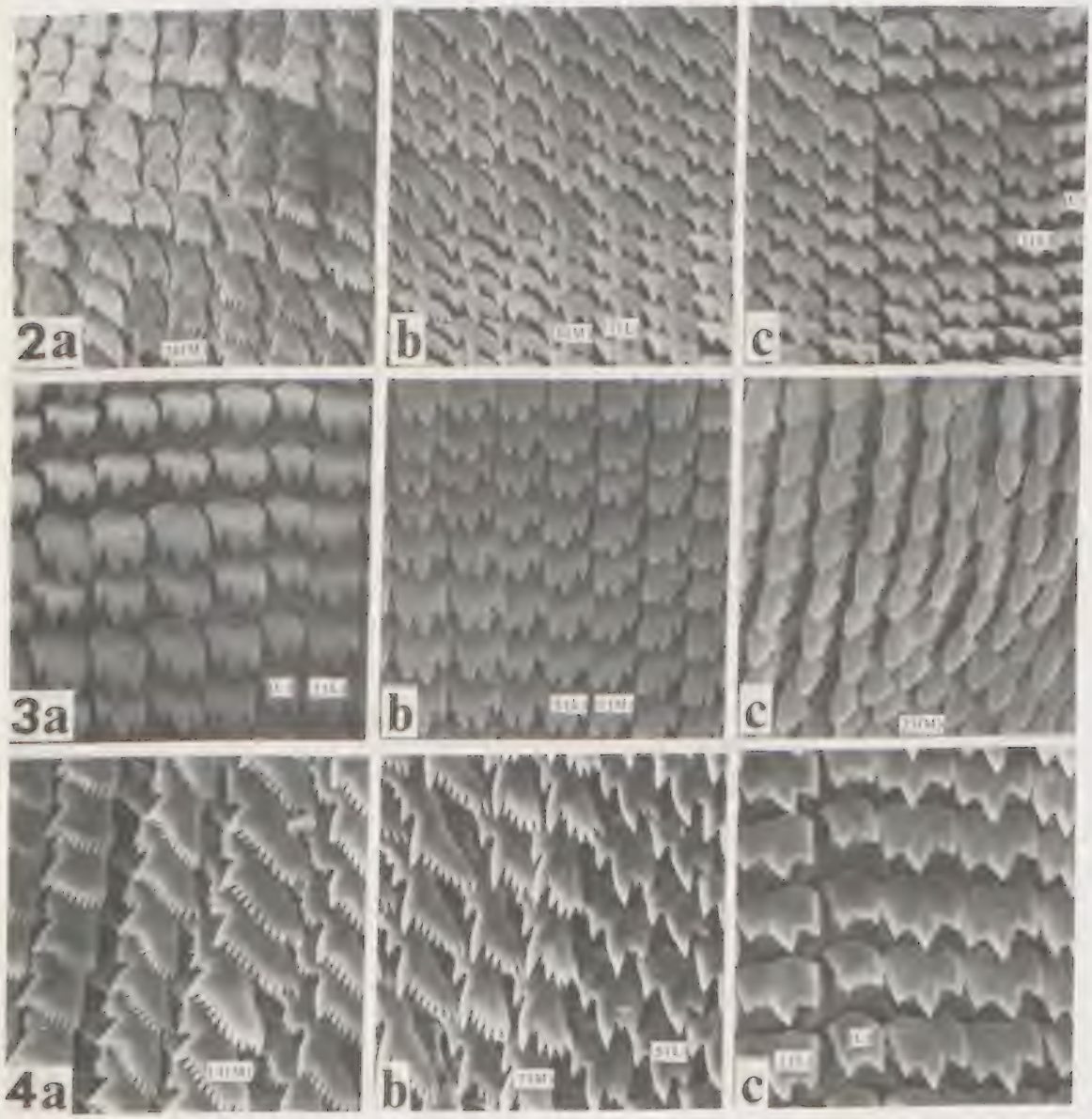
OBSERVATIONS

Bulinus tropicus (Figs. 2, 14a, 15a)

The central tooth is bilaterally symmetrical, with two equal-sized cusps. Sometimes on the outside of each of these cusps there are two tiny denticles or corrugations. A minor cusp ("interstitial cusp") or denticle frequently occurs between the two major cusps.

The lateral teeth are basically tri-cuspid. Usually there is a small denticle between the entocone and the mesocone, and between the mesocone and the ectocone. Occasionally there are two denticles between the mesocone and the ectocone. The entocones and ectocones of each of the lateral teeth are almost the same size. They are slightly smaller than the mesocone. The more prominent mesocone has the evenly tapering contour referred to by Mandahl-Barth (1957) as "triangular".

There is a gradual transition from the lateral to the marginal teeth, but perhaps the beginning of the marginal teeth can be taken as where the entocone begins splitting into two cusps. The marginal teeth are elongate and comb-like, thereby being distinctly different from the lateral teeth. They assume the marginal-tooth form most distinctly in the majority of the rows at the 8th tooth on each side of the central tooth. Here the entocone splits into two or sometimes three cusps. Actually, tooth 8 is a transitional tooth. Tooth 9 is very decidedly a marginal tooth. Here the entocone divides into four (sometimes five) roughly equal-sized cusps. At tooth 9, the ectocone also is divided into a number of cusps: two major cusps and up to four minor cusps or denticles. The single-cusped mesocone maintains its integrity throughout the row. As the marginals proceed outward, the four-cusped entocone becomes five-cusped generally from tooth 10 through tooth 13, and then either retains this condition or adds a cusp (sometimes two; or occasionally loses a cusp). The dominance of the mesocone continues, but progressively diminishes with each tooth outwardly through the marginals. By tooth 32, the mesocone is hardly more prominent than the inner-most entocone cusp. Here, the prominence of the mesocone is marked not by its size but by its continuation on to the hook-body as an anteroposterior ridge. Because of the increased prominence of the entocone cusps, the reduction of the mesocone, the mesoconal ridge and the reduction and shift in position of the ectocone cusps, the aspect of the marginal tooth is considerably changed by tooth 31. Here the functional shape of the tooth is more like a hoe (i.e., the cutting edge is broadly



FIGS. 2-13. Scanning electron microscope photographs of planorbid radular teeth. FIG. 2. *Bulinus tropicus*. a, Marginal teeth; b, marginal and lateral teeth; c, lateral and central teeth. FIG. 3. *B. truncatus*. a, Central and lateral teeth; b, lateral and marginal teeth; c, marginal teeth. FIG. 4. *Isidorella newcombi* (nr. Morundah). a, Marginal teeth; b, marginal and lateral teeth; c, lateral and central teeth. Numbers on the individual teeth refer to vertical rows counted consecutively distally from the central tooth.

Abbreviations: C = central tooth; L = lateral tooth; M = marginal tooth.

rounded rather than pointed). From tooth 32 until 39 (at the edge of the radular ribbon), the marginal teeth become progressively narrower, smaller, and their axis more anteroposterior. The several outer-most marginal teeth could be described as almost rudimentary.

Bulinus truncatus (Figs. 3, 14b, 15b)

The central tooth of *Bulinus truncatus* has the same appearance as that of *B. tropicus*. It is bicuspid, often with a small denticle between the two cusps, and occasionally with a tiny denticle on the outer side of each cusp near the hook-body.

The lateral teeth are also very similar to those of *Bulinus tropicus*. They differ in that the shape of the mesocone is more generally that of an "arrow-head", and in our specimen the transition of the teeth to marginals begins at the 6th tooth from the center.

At tooth 6, the entocones begin dividing into two cusps. The cusps of the entocones continue to become more numerous and smaller as the teeth progress outward on the radular row. By tooth 8 there are four entocone cusps, five by tooth 9, and five or six by tooth 12. As the number of the entocone cusps increase in number and the mesocone decreases in size, the marginal teeth take on a comb-like appearance, similar to that seen in the outer marginals of *Bulinus tropicus*. By the outer-most marginal (tooth 31), the tooth has become very reduced in size, almost rudimentary.

Isidorella newcombi (near Morundah) (Figs. 4, 14c, 15d)

The central teeth are similar in appearance to those of *Bulinus tropicus* and *B. truncatus*, except that they lack small inter-cusp denticles and lateral corrugations.

The tricuspid lateral teeth are also similar to those of *Bulinus*, but there is much less tendency to have denticles between the cusps. A denticle is rarely seen between the entocone and the mesocone, but a very small denticle is more common on the side of the entocone. The cusps are triangular or spade shaped. The hook-body of the lateral tooth is very slightly corrugated on both lateral edges.

The transition to marginal teeth begins at tooth 6. From here outward the entocones of the lateral teeth split progressively into 2-11 cusps, which on any particular tooth are nearly even in size and shape. Teeth 7-19 have a very distinct comb-like appearance. Tooth 6 is transitional, but tooth 7 is distinctly marginal in character. The mesocone retains its identity to tooth 20, but is merged with the entocone on the very simplified tooth 21. At tooth 20, the outer entocone cusps are fused, and on tooth 21 the multiple entocone cusps have lost their identity, all being fused along with the mesocone into one larger axe-like cusp (i.e., the functional edge is almost straight rather than rounded or pointed).

The ectocones have noticeable denticles on their outer margins at transitional tooth 6. From tooth 7, the ectocone is divided into 2-5 (rarely 6) cusps. These cusps are secondary in prominence to the cusps of the entocones and mesocones. At tooth 18, the ectocones are greatly reduced, their cusps fused, and at tooth 19 outward the ectocone is usually hardly more than a nub.

Isidorella newcombi (Spencer's Gorge) (Figs. 5, 14d, 15c)

The bicuspid central tooth is similar to that of *Isidorella newcombi* from near Morundah, including lacking a denticle between the cusps and lacking corrugated lateral edges.

The lateral teeth are tricuspid, with prominent, somewhat tumid mesocones. The distal margins of the mesocones (i.e., the margins on the lateral side) are noticeably longer and more convex than the proximal margins (i.e., the margins on the medial side). The mesocone rarely has denticles or corrugations on its lateral edges.

The marginal teeth start rather abruptly at tooth 12 when the entocone splits into two major and one or more minor cusps or denticles. Continuing outward, the entocone cusps increase to three at tooth 13, four at tooth 14, and five at tooth 19 or 20. Sometimes the entocone cusps have small denticles between them. From tooth 14 on, the entocone cusps are nearly equal in size, projecting a comb-like appearance. However, they do not have quite the uniformity as those of *Isidorella newcombi* from near Morundah (and are fewer in number). The single-cusped mesocones maintain their identity throughout the horizontal radular row, but become progressively smaller distally (laterally), equalling the entocone cusp size at tooth 26.

Physastra concinna (Figs. 6, 14e, 15e)

The central tooth is bicuspid, with a small denticle between the cusps. The lateral edges of the cusps are corrugated.

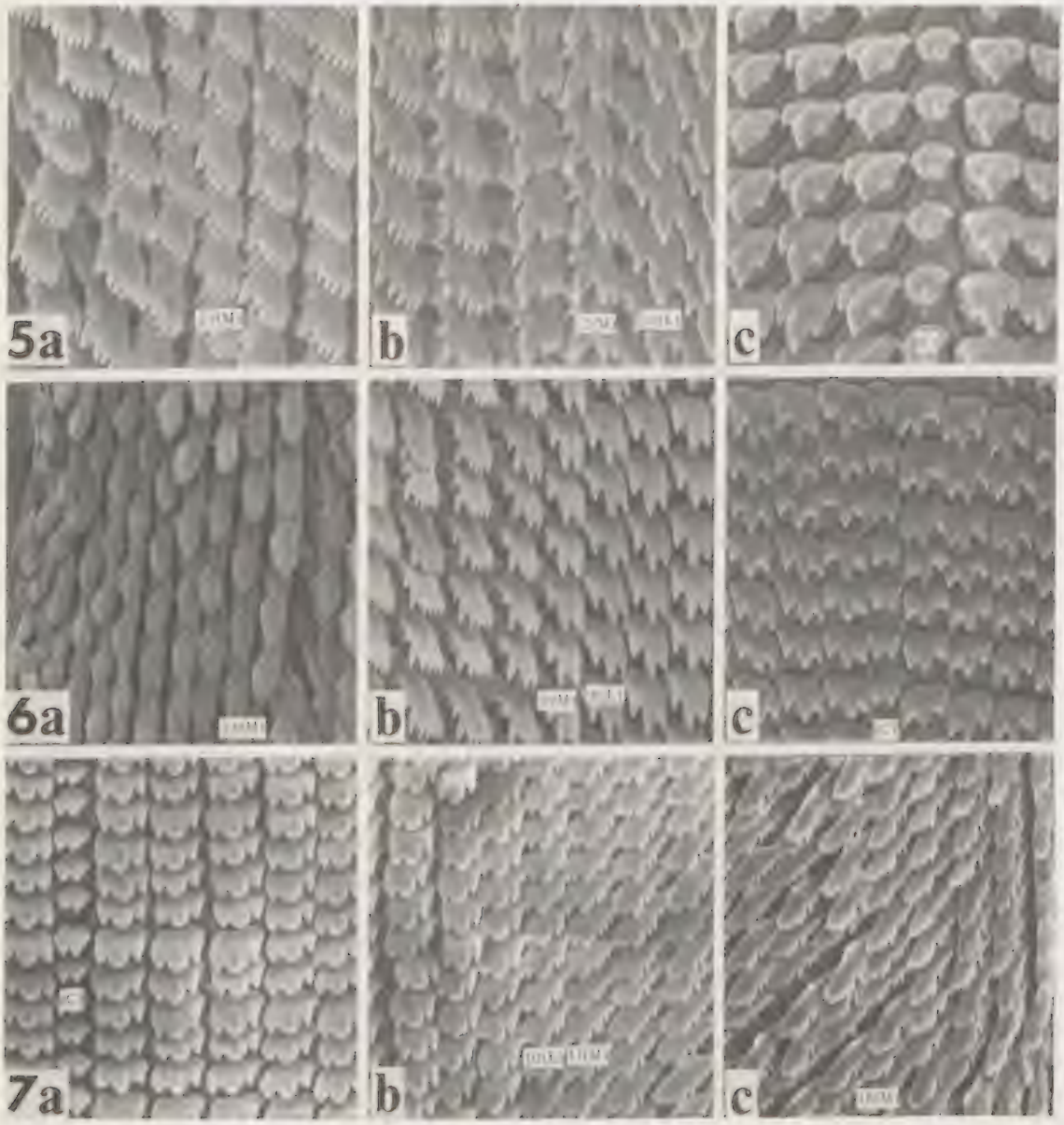


FIG. 5. *Isidorella newcombi* (Spencer's Gorge). a, Marginal teeth; b, marginal and lateral teeth; c, lateral and central teeth. ca X470. FIG. 6. *Physastra concinna*. a, Marginal teeth; b, marginal and lateral teeth; c, lateral and central teeth. ca X470. FIG. 7. *Planorbella trivolvis*. a, Central and lateral teeth; b, lateral and marginal teeth; c, marginal teeth. ca. X260.

The lateral teeth are tricuspid, but differ from the preceding three species in that the mesocones of the proximal (i.e., more medial) lateral teeth are narrower (rather than wider) than the entocones and ectocones. The ento- and ectocones are triangular, and the mesocone is narrowly spade shaped. Denticles are noticeable on some of the ento- and ectocones. The marginal teeth begin with tooth 9, which is a transitional tooth. The entocone of tooth 9 is divided into a major and a minor cusp, and the hook-body and base are elongated horizontally. At tooth 8 the denticles of the ectocones are becoming more prominent, and this prominence increases on teeth 9, 10 and 11.

The marginal teeth are elongate and comb-like, becoming more so distally (i.e., as they progress laterally). Also, the number of cusps of the entocones increases distally; the entocone

of tooth 10 has two major cusps and two to four minor cusps or denticles; tooth 11 has four (sometimes five) major cusps and one or two minor cusps or denticles; tooth 13 has five major cusps and one to three minor cusps or denticles; tooth 15 has six major cusps and one to two minor cusps; tooth 17 has eight nearly equal-sized cusps; tooth 21 has nine cusps; tooth 24 has 10 or 11 cusps. The entocone (and meso- and ectocone) cusps progressively decrease in size distally. At the outermost edges of the radula they become obsolete. The single-cusped mesocones retain their identity to the lateral radular margins and generally are larger than the cusps of the ecto- and entocones. In most of the marginal teeth, one of the ectocone cusps is larger than the rest.

Planorbella trivolvis (Figs. 7, 14f, 15f)

The central tooth has two major cusps, which are equal in size and triangular in shape.

The lateral teeth are tricuspid. The mesocone is rounded, wider than the other cusps. The entocone is almost as long as the neighboring mesocone and is spade shaped. The somewhat smaller ectocone is triangular in shape and often has denticles or corrugations along its distal margin. At tooth 9, a minor cusp develops, increasing to two at tooth 10. These are transitional teeth. No denticles were observed between the cusps.

The marginal teeth are elongated horizontally (laterally). They begin after tooth 10 with a division of the entocone into two cusps and an increase in the number of the ectocone cusps. After tooth 11, the entocone splits into three to six cusps. The single-cusped mesocone retains its prominence nearly to the outer margins of the radula. By tooth 14, the ectocone cusps have increased generally to six or more. They become more needle-like and uneven in size near the lateral margins of the radula. The ectocone cusps of the marginal teeth are more prominent than the cusps of the entocones, a noticeable difference from all the preceding species.

Helisoma anceps (Figs. 8, 14g, 15g)

The central tooth is bicuspid and, like all the above species, the major cusps of the central tooth are equal in size and shape. Both lateral edges near the bases of the cusps are corrugated to form small cusps or denticles.

The lateral teeth are tricuspid. On the first lateral teeth, the mesocone, which is elongate and spade shaped, is the most prominent cusp. The entocones are also prominent, but slightly shorter, a bit narrower, triangular, and with a series of serrations or denticles on the margin next to the central tooth. The ectocones are reduced. Between the ectocones and mesocones are one or two denticles. Denticles rarely occur between the entocones and mesocones. Both of the lateral edges of the lateral teeth are noticeably corrugated and serrated.

The marginal teeth begin with tooth 7, which also might be considered to be a transitional tooth. It is narrower and more claw-like than tooth 6. The entocone splits into two cusps at tooth 8. At tooth 9, the entocone may be split into as many as four cusps, and by tooth 13 into as many as six cusps. These cusps may be regular in shape, but more often they are irregular. From tooth 14 outward, the cusps have a tendency to fuse. These teeth become excessively elongate and resemble scoop-like trowels. A conspicuous aspect of the entocones of teeth 1-11, and sometimes 12, is the series of denticles along their proximal margins. The single-cusped mesocones retain their prominence almost to the lateral edges of the radula. The ectocones, which at the first lateral tooth already have several minor cusps in addition to the major cusp, continue in this fashion to tooth 20. They have less tendency to fuse in the outer marginals than do the entocones.

Amerianna carinata compar (Figs. 9, 14h, 15h)

The central tooth is bicuspid with long narrow cusps, each of which is flanked on the outside by a small cusp or denticle.

The lateral teeth have three narrowly spade-shaped major cusps, and a smaller cusp present

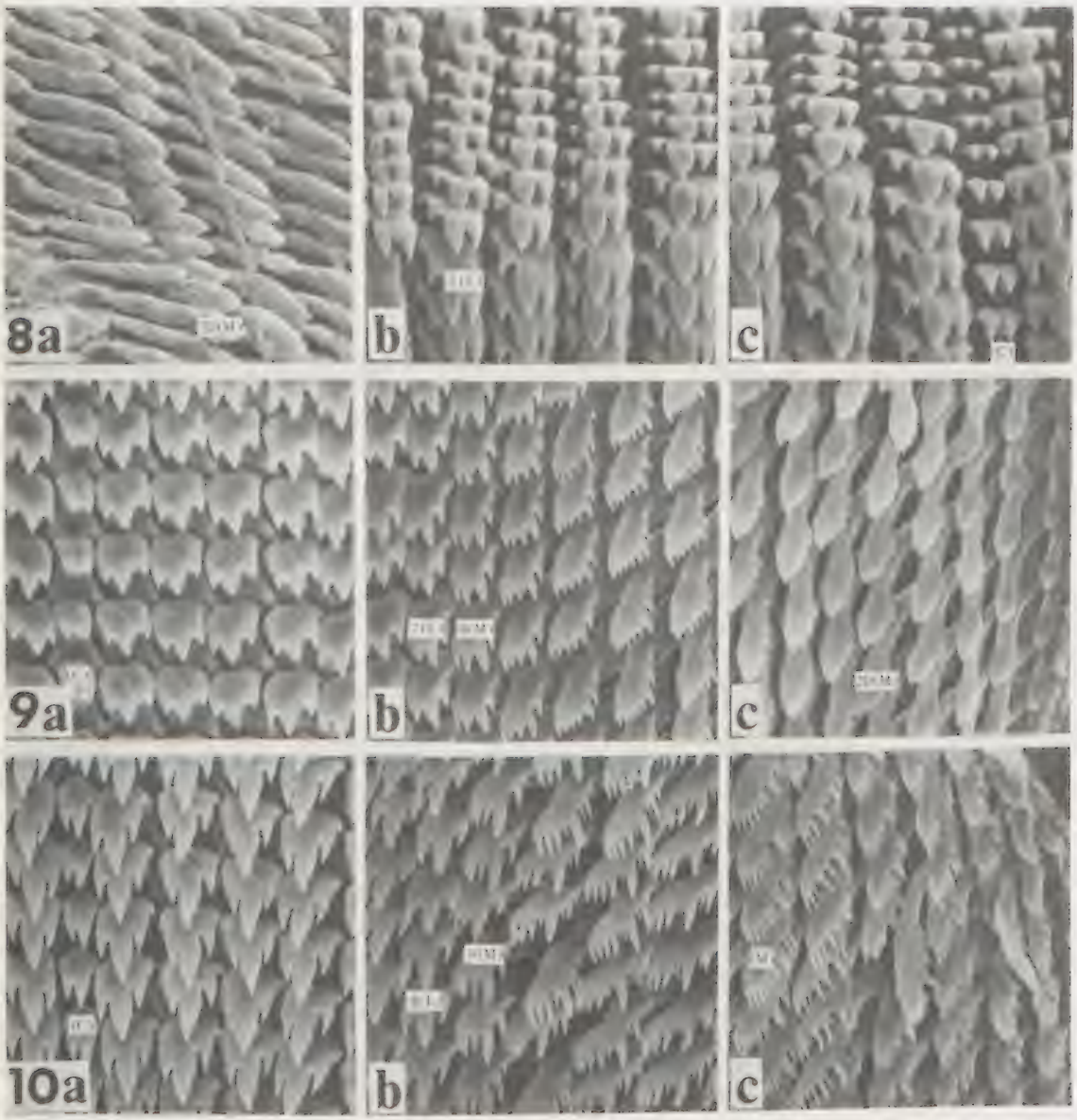


FIG. 8. *Helisoma anceps*. a, Marginal teeth; b, marginal and lateral teeth; c, lateral and central teeth. ca X470. FIG. 9. *Amerianna carinata compar*. a, Central and lateral teeth; b, lateral and marginal teeth; c, marginal teeth. ca. X705. FIG. 10. *"Isidorella" sisurnia*. a, Central and lateral teeth; b, lateral and marginal teeth; c, marginal teeth. ca. X705.

on the two lateral edges of the hook-bodies. One very prominent denticle lies between the ectocone and mesocone, and a more minor one sometimes occurs between the entocone and the mesocone. This minor cusp becomes very persistent on the outer laterals. The three major cusps are narrowly spade shaped.

The marginal teeth begin with tooth 8, which is a transitional tooth. Here the base and hook-body become more elongate horizontally (laterally), the inter-cusp denticle is retained, and the entocone divides into two equal-sized cusps. At tooth 9, the entocone divides into three equal-sized cusps, the outer one flanked on each side by a denticle. Tooth 10 has four

equal-sized entocone cusps, between each of which is a minor cusp or denticle. Teeth 11 and 12 have the same arrangement, but with six entocone cusps. Tooth 13 has seven equal-sized entocone denticles. The remaining marginal teeth continue in this fashion to the margin, with some denticles becoming as prominent as the cusps, and the cusps getting smaller on the outer teeth. The regularity in size of the entocone cusps of the marginals give these teeth a distinctive comb-like appearance. At tooth 20, nearly all the denticles or minor cusps have become equal in size to the major cusps. Here the entocone cusps number 10-12. The single-cusped mesocone retains its identity nearly to the outermost marginal tooth. The ectocones are not very prominent, but they persist out to tooth 20, then become obsolete.

"Isidorella" sisurnia (Figs. 10, 14i, 15i)

There are four cusps on the central tooth, two of which are very prominent. On the outside of each of the major cusps are two smaller cusps, and between the two major cusps there is often a denticle. The right major cusp is larger than the left, making the central tooth asymmetrical.

The lateral teeth are basically tricuspid, with denticles between the major cusps, and one or several minor cusps on the distal (outer) side of the ectocone. The proximal (inner) edge of the entocone has corrugations or denticles. The mesocone is prominent. The sides of the mesocones are either rounded, angular or straight. The proximal side is shorter than the distal. The denticle between the mesocone and ectocone is very prominent and deeply recessed. Tooth 8 is somewhat transitional, but basically similar to the other lateral teeth.

The marginal teeth begin with tooth 9. They are elongate, comb-like, with somewhat irregular, sharp, dagger-like cusps. At tooth 9, the entocone is split into three approximately equal cusps, the single-cusped mesocone maintains its prominence, and the ectocone consists of a large cusp and several smaller ones. The prominent denticle between the mesocone and ectocone persists. Progressively outward to the radular margins, the entocone and ectocone cusps increase in number. For example, on one of the teeth in longitudinal row 17, there are seven entocone cusps and eight ectocone cusps. Near the radular margins the cusps decrease in size, but the mesocone retains its conspicuousness and identity. The ectocone cusps of the marginal teeth match and sometimes surpass the entocone cusps in prominence.

Camptoceras cosmeta (Figs. 11, 14j, 15j)

The central tooth has four cusps, two of which are prominent, and of these two the left cusp is larger than the right one. On the outside of each of the two major cusps are two closely attached smaller cusps.

The lateral teeth have two large cusps and two or three smaller cusps. The mesocone is the largest in size, followed by the ectocone. Between the mesocone and ectocone is a prominent denticle. The entocone is reduced. Distal to the ectocone is one or two smaller cusps.

If the marginal teeth are considered to begin where the entocone starts splitting into two cusps, then this happens at tooth 11, although all teeth in this vertical row, as well as the next several, do not consistently split. The entocone has three cusps at tooth 15 and four at tooth 16. Some teeth in vertical row 17 have five cusps, and some have six. At tooth 18 there is a general reduction or fusion of cusps, and by tooth 20 the entocone cusps are mostly fused or obsolete. The ectocone and accessory cusps continue in prominence from the laterals out to tooth 21. On the marginals, they increase in number to four to six, then diminish in the several outermost teeth. The mesones retain their prominence from the first laterals through tooth 20.

Bayardella johni (Figs. 12, 14k, 15k)

The central tooth has one major cusp, somewhat asymmetrically placed, flanked on each side by two cusps (or perhaps better described as a cusp and a denticle). The cusps closest to the large median cusp are larger than the two outer cusps or denticles on each side.

The lateral teeth have four cusps. The mesocones are quite large, and are excessively developed from the second lateral tooth out to the marginal teeth. They are long and dagger or

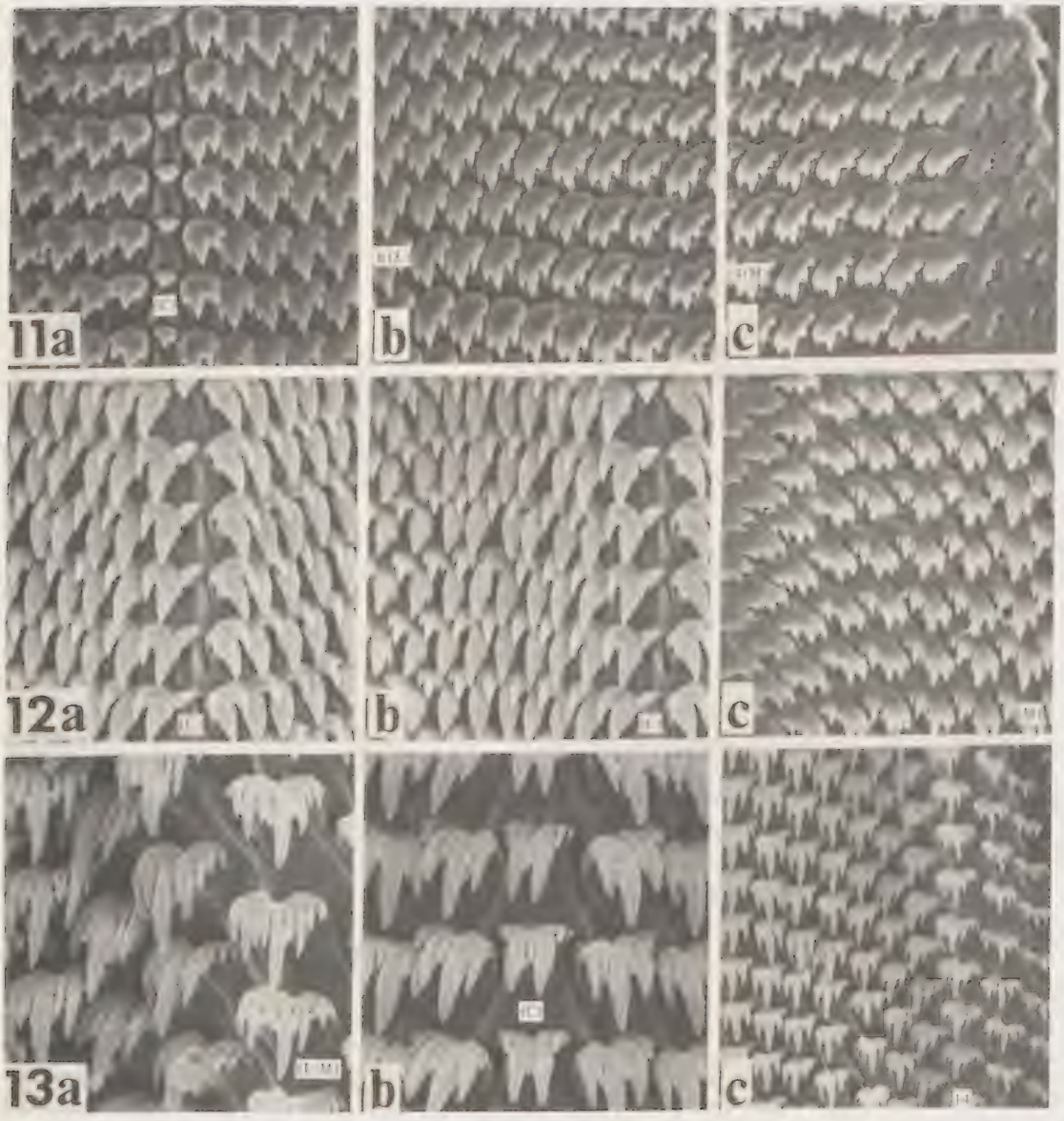


FIG. 11. *Camptoceras cosmeta*. a, Central and lateral teeth; b, lateral and marginal teeth; c, marginal teeth. ca. X470. FIG. 12. *Bayardella johni*. a, Central and lateral teeth, ca. X660; b, central, lateral and marginal teeth, ca. X610; c, marginal teeth, ca. X610. FIG. 13. *Gyraulus essingtonensis*. a, Lateral/marginal teeth, ca. X2820; b, central and lateral/marginal teeth, ca. X2820; c, lateral/marginal teeth, ca. X1410.

sickle-like. The entocones of the first lateral teeth are very small. The ectocones are well developed. Distal to the ectocones is another smaller cusp. Between some of the mesocones and ectocones is a small denticle. On the second lateral teeth this denticle is well developed, forming a small but distinct cusp, equal in size to the cusp distal to the ectocone. The ectocone together with these two flanking cusps constitute a subunit of the tooth, a condition which persists nearly to the lateral edges of the radula. This ectoconal subunit is nearly separated from the mesocone-entocone subunit in most of the lateral teeth.

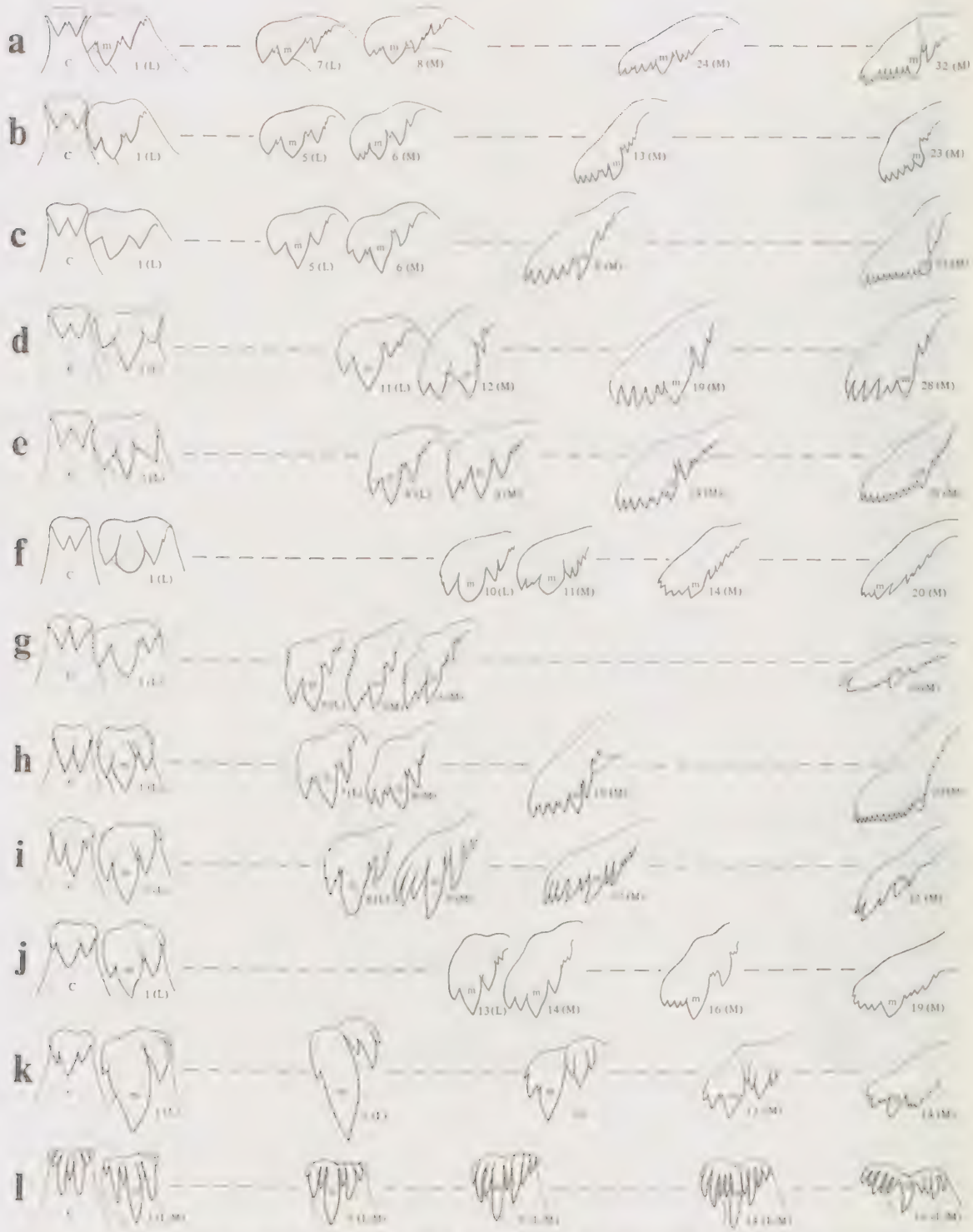


FIG. 14. Planorbid radular teeth. a, *Bulinus tropicus*; b, *B. truncatus*; c, *Isidorella newcombi* (nr. Morundah); d, *I. newcombi* (Spencer's Gorge); e, *Physastra concinna*; f, *Planorbella trivolvis*; g, *Helisoma anceps*; h, *Amerianna carinata compar*; i, *"Isidorella" sisurnia*; j, *Camptoceras cosmeta*; k, *Bayardella johni*; l, *Gyraulus essingtonensis*. The number under each tooth designates its consecutive position distally from the central tooth.

Abbreviations: C = central tooth; L = lateral tooth; M = marginal tooth; m = mesocone.

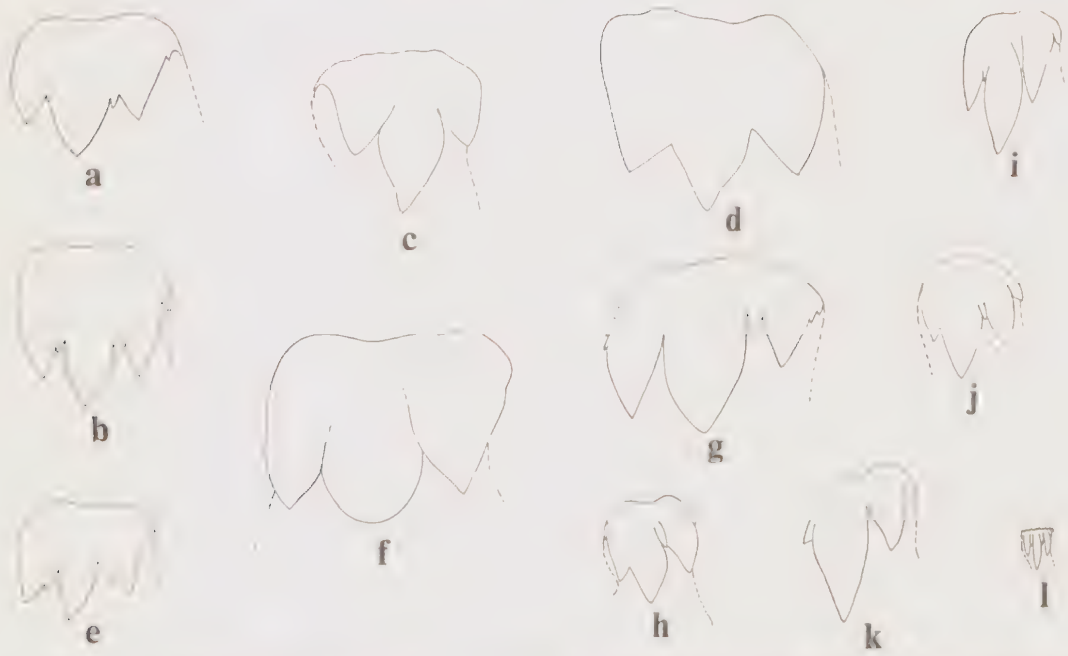


FIG. 15. The first right lateral teeth of planorbid snails to show relative sizes. a, *Bulinus tropicus*; b, *B. truncatus*; c, *Isidorella newcombi* (Spencer's Gorge); d, *I. newcombi* (nr. Morundah); e, *Physastra concinna*; f, *Planorbella trivolvis*; g, *Helisoma anceps*; h, *Amerianna carinata compar*; i, *"Isidorella" sisurnia*; j, *Camptoceras cosmeta*; k, *Bayardella johni*; l, *Gyraulus essingtonensis*. All teeth X1360.

The transition from lateral tooth to marginal tooth is rather gradual and is most noticeable where the mesocones are reduced, losing their sickle-like appearance, the ectocone cusp is reduced, and the entocone emerges from its near obscurity. This is especially noticeable at tooth 9 or 10, both transitional teeth.

The marginal teeth change gradually from the lateral teeth by a diminution of the mesocone and ectocone, and an increase in prominence of the entocone. The entocone cusps increase to two, then to three, and finally to four (occasionally five) in the outermost several marginals. Sporadically from tooth 10 to tooth 14, the cusps between the mesocone and ectocone change in number from one to two to three cusps. At tooth 15, these cusps and the ectocone are all about the same size.

Gyraulus essingtonensis (Figs. 13, 14l, 15l)

The central tooth has a primarily bicuspid aspect, with two major cusps which are very long and dagger-like. There is one deeply cut minor cusp between the major cusps and two weaker minor cusps on the lateral sides of the two major cusps. Sometimes there may be an additional smaller minor cusp or denticle, but that is not normal or consistent.

The lateral teeth have primarily a tricuspid aspect, with three long and dagger-like major cusps. Between these, and on both lateral edges of each tooth, are well-developed minor cusps, which are similar in appearance to the major cusps, but they are smaller and shorter. There is one minor cusp on the medial side of the entocone and two minor cusps on the outer side. This condition continues nearly to the outer edges of the radula; the transition between the laterals and marginals is so gradual, and distinctive laterals occur so close to the outer margins of the radula, that it seems pointless to distinguish between lateral and marginal teeth. At vertical row 14, a few teeth have two minor cusps between the mesocone and entocone, and some teeth have an additional cusp or denticle at the distal margin. These same conditions can be seen on an occasional tooth in vertical row 13, but they become even more persistent

on the teeth of vertical row 15, where there may be one or two additional cusps present as well. At vertical row 15, tooth development diminishes and the large difference in size of the major and minor cusps as seen on more proximal teeth is reduced. At row 16, this tendency is accelerated, and, except for the mesocone, the size difference between major and minor cusps is small. The mesocone is also considerable reduced. The teeth of vertical row 17, at the outer margin of the radula, are nearly rudimentary.

Radular teeth similar to those described above for Australian *Gyraulus essingtonensis* have been shown for Eurasian *Gyraulus* by Meier-Brook (1979), except for the species of ancient lakes Ohrid and Prespa, which had aberrant radulae.

DISCUSSION

According to F.C. Baker's (1945) classification of the Planorbidae, the species observed in the present study would be arranged as follows.

Family Planorbidae
- Subfamily Planorbinae
  - *Gyraulus essingtonensis*
- Subfamily Helisomatinae
  - *Helisoma anceps*
  - *Planorbella trivolvis*

Family Bulinidae
- *Bulinus tropicus*
- *Bulinus truncatus*
- *Amerianna carinata compar*
- *Bayardella johni*
- *Camptoceras cosmeta*
- *Isidorella newcombi*
- *"Isidorella" sisurnia*
- *Physastra concinna*

Baker (1945) considered nearly all the non-planate Planorbidae, and the planate *Indoplanorbis*, to belong to a separate but closely related "family" Bulinidae. His concept of this family included not only *Bulinus* and *Indoplanorbis*, but apparently also *Amerianna, Camptoceras, Isidorella* and *Physastra* as well, judging from his geographical distribution as given for the Bulinidae on page 196, and the omission of these genera from his monograph on the Planorbidae. However, this placement by Baker of the later four genera in the Bulinidae must have been by assumption only, because more recent studies (Hubendick, 1955) show that they do not have the main characteristic of the "family", i.e., the type of penis described by Larambergue (1939a,b) and later referred to by Hubendick (1955) as an "ultra-penis". Baker must have been guided by the non-planate aspects of their shells. By including the Antilles in the geographical distribution of the "family", he indicates that he would have included the non-planate *Plesiophysa* in the Bulinidae, too, and therefore, by analogy to its very similar shell, the more recently described *Bayardella* (Burch, 1977) of Australia.

Baker (1945) figured the radulae of various planorbid snails, and noted that some members of the subfamily Planorbinae (as he understood it) had "serrated marginals placed high up on the reflection." He listed the genera with radulae exhibiting this type of marginal teeth as *Planorbis, Anisus, Armiger, Bathyomphalus* and *Gyraulus*.

Following Hubendick's (1955) classification of the Planorbidae, the species observed in the present study would be arranged (as far as is presently known from the characters they possess) as follows.

Family Planorbidae

Subfamily Planorbinae

Planorbis tribe [Tribe Planorbini]

Gyraulus essingtonensis

Ameriana tribe [Tribe Amerianini]

Amerianna carinata compar

[*Camptoceras* tribe] [Tribe Camptoceratini]

Camptoceras cosmeta

Helisoma tribe [Tribe Helisomini or Helisomatini]

Helisoma anceps

Planorbella trivolvis

Physastra tribe [Tribe Miratestini]

Physastra concinna

Subfamily Bulininae

Bulinus tropicus

Bulinus truncatus

Isidorella newcombi

"Isidorella" sisurnia

Subfamily Plesiophysinae

Bayardella johni

It should be noted that Hubendick's *Planorbis* tribe has exactly the same set of genera that Baker (1945) noted as having "serrated marginals placed high up on the reflection", and that the other genera of Hubendick's Planorbinae have what Baker would call "claw-like marginals on a long reflection". Hubendick's Planorbinae contains, in addition to the *Planorbis* tribe, all of the other genera Baker (1945) placed in the Planorbinae, and those genera of the Helisomatinae, Planorbulinae and Segmentininae as well.

Most of the species observed in our present study have bicuspid central teeth, which is typical of the Planorbidae. Of these species, several sometimes or frequently had a small denticle between the two cusps, several species had a small denticle on each side of the cusps near their attachment to the hook-body, and one species (*Helisoma anceps*) had corrugated anterior lateral edges of the two cusps, resulting in several small denticles on each side. These small cusps may be of sporadic occurrence, or are not consistently present, and so little attention is paid to them as taxonomic characters.

Greater significance may be given to the central teeth which deviate from the above bicuspid condition. Species with such central teeth are *"Isidorella" sisurnia, Camptoceras cosmeta, Bayardella johni* and *Gyraulus essingtonensis*. Of these, the first two species have central teeth with two main cusps, but on the outer side of each of these cusps is a smaller cusp, i.e., the central teeth have four cusps rather than the usual two. Also, it is quite noticeable that these two species have asymmetrical central teeth, in which one of the major cusps has a greater development. In *"I." sisurnia*, the right major cusp is the larger, while in *C. cosmeta* it is the left cusp that is largest. In *B. johni*, this asymmetry has progressed further, so that the enlarged left cusp becomes practically a singular medianly placed mesocone. This large, nearly central cusp is flanked by two smaller cusps, of which the right one is slightly larger. On the outside of each of these smaller cusps is another even smaller cusp, perhaps small enough to be considered as merely denticles (in which case the central tooth would be called three-cusped, rather than five-cusped as in the original description).

The central teeth of *Gyraulus essingtonensis* are quite different from any of the other Planorbidae studied. Although the central teeth of *Gyraulus* might be called bicuspid because of their two most prominent cusps, the other five cusps, although smaller, are also well

developed. Thus, with two major and five minor cusps, *G. essingtonensis* is basically seven-cusped. This type of central tooth was not described by Baker (1945) or Hubendick (1955) for *Gyraulus*.

The lateral teeth of most of the species studied are basically similar. They are tricuspid, with the mesocone being a bit larger (longer and wider) than either the entocone or ectocone. In *Physastra*, although the mesocone is slightly longer, it is narrower than the other two cusps. There are some slight differences in the shape of the cusps among the various species, from triangular to spade shaped and arrowhead shaped. In *Planorbella*, the end of the mesocone is rounded. In some species, there is a tendency for denticles to appear between the major cusps of the lateral teeth. This is especially the case in *Bulinus*. In *Helisoma anceps*, the lateral edges are corrugated or serrated.

The lateral teeth of five of the Australian species differ from those discussed above. In *Camptoceras cosmeta*, *Amerianna carinata compar* and *"Isidorella" sisurnia*, there is a minor cusp on the outside of the ectocone, and, in the latter two species, there is a minor cusp on the outside of the entocones as well. These extra cusps give a different aspect to the lateral teeth. But just as noticeable in these three species is a very well-developed denticle in a groove between the mesocone and the ectocone.

The lateral teeth of *Bayardella johni*[2] are even more different. The mesocones are excessively developed, and the entocones are exceptionally small. [Because of the very small size of the entocones and difficulties inherent in light microscopy, the entocones were not observed during the original description of *B. johni*. Therefore, the mesocones were mistakenly taken to be entocones, and the denticles between the mesocones and ectocones to be mesocones. The superior resolving power of the SEM has clarified the cusp condition in this species.] The ectocone is well developed, and on its outside margin is a smaller cusp. From the second lateral tooth on, the denticle between the mesocone and ectocone becomes highly developed, being noticeably larger than the entocone. Also, beginning with the second lateral tooth, the division between the mesocone and ectocone is accentuated, so that each tooth of the lateral teeth appear to be divided into two halves, a proximal half consisting of the very large mesocone and the tiny entocone, and a distal half comprising the ectocone flanked by the exceptionally developed denticle and the lateral cusp.

Hubendick (1955) referred to the first lateral tooth of *Plesiophysa ornata* as being "quadricuspid". This type of first lateral tooth is also found in *Camptoceras cosmeta* (Fig. 14j), and derivations of this type are found in *"Isidorella" sisurnia* and *Amerianna carinata compar*, and, although much more highly modified, also in *Bayardella johni*. Judging from the morphology of the first lateral teeth, there seems to be an obvious relationship between the four Australian species: *A. carinata compar*, *"I." sisurnia*, *C. cosmeta* and *B. johni*. In this series, *B. johni* has progressed farthest, having an exceptionally large mesocone, a reduced entocone, and a tendency for the lateral teeth to be divided roughly into two halves or subunits between the mesocone and ectocone. This relationship seems to be borne out in the morphology of the central tooth of the latter three species in that their cusp development is asymmetrical. This asymmetrical cusp development of the central tooth is certainly a stage in the similar development of the single median cusp flanked by secondary cusps of *Plesiophysa* as described by Bland & Binney (1873), Fischer (1887), Bequaert & Clench (1939), Hubendick (1949, 1955), Richards & Ferguson (1962) and Michaelson (1969). [The latter author described the central tooth of Bland & Binney's (1873) specimen as having six cusps ("typical of the genus *Plesiophysa*"), but all authors, including Binney and Bland, described *five* cusps for *Plesiophysa*.]

Radular tooth characters, coupled with divergent shell characters, would indicate that

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[2] *Bayardella johni* was originally assigned provisionally to *Plesiophysa* because of similarities in shells and central radular teeth (Burch, 1977). However, it is doubtful if *B. johni* is closely related to that Neotropical genus.

"Isidorella" sisurnia is not closely related to *I. newcombi*, but is probably more closely related to *Bayardella johni* and *Camptoceras cosmeta*. The latter two species, by both radular and shell characters, would seem to be rather closely related. Once they are studied, it will be interesting to see what relationships anatomical characters indicate.

It is interesting to note the similarities in the marginal teeth of some of the species, viz., the type of tooth with cusps in a more or less straight, even cutting [or raking] edge, which is found in *Bulinus tropicus, B. truncatus, Isidorella newcombi, Physastra concinna* and *Amerianna carinata compar*. A modification of this shape, with an enlarged median cusp, is seen in *Camptoceras cosmeta* and *Bayardella johni*. A narrow, slanting marginal tooth is seen in the American *Planorbella trivolvis* and *Helisoma anceps*, and in the Australian *"Isidorella" sisurnia* as well. None of these species had marginal teeth approaching those of *Gyraulus essingtonensis* in form.

In *Gyraulus essingtonensis*, the morphology of the lateral teeth grades so insensibly into that of the teeth at the margin of the radula, that it does not seem justifiable to designate "lateral" teeth as separate from "marginal" teeth. In such cases, the practice is either to refer to all teeth other than the central teeth simply as "marginals" (e.g., see Cox, 1960) or as "laterals" (e.g., see Fretter & Graham, 1962; Wu, 1972). However, for convenience, we refer to them as "lateral/marginal" teeth.

The lateral/marginal teeth of *Gyraulus essingtonensis* are much different from the teeth of any of the other species discussed above. The cusps are relatively longer and narrower, and between the major cusps are denticles so well developed that they might be considered to be secondary cusps rather than mere denticles. Yet, the lateral/marginal teeth are basically tricuspid, in that each tooth has three prominent major cusps. As observed by Baker (1945), and re-affirmed by Hubendick (1955), the distal lateral/marginal teeth of *Gyraulus* do have a different character than that of the groups represented by the other species studied here. This type of lateral/marginal tooth may well reflect a major taxonomic division, as Hubendick (1955) contended (". . . all genera with short marginals [i.e., similar to *Gyraulus*] represent one main branch within the subfamily [Planorbinae]"). However, any such conjecture should take into account the complete range of other morphological characters in conjunction with evolutionary modifications caused by food preferences, and how food may relate to specific tooth/cusp types.

In regard to relative size, the teeth of *Gyraulus essingtonensis* are much smaller than those of the other planorbid species (Fig. 15), and this undoubtedly is related to *Gyraulus*' smaller body size. The tooth-cusp morphology may be a reflection not only of small body size in relation to food size, but to qualitative differences in food as well.

Since little or nothing is known about the feeding habits and food of these planorbid snails, it is difficult to interpret what functional advantages a central tooth with asymmetrical cusps would have, or one with a single median cusp flanked by four smaller lateral cusps, or one with two symmetrical and equally developed median cusps. Lateral teeth with broad, blunt mesocones, such as those seen in *Planorbella trivolvis*, would seem better suited to scraping rather than cutting, indicating that this species may feed more on algae scraped from underwater surfaces than on tissues cut from aquatic plants. Yet this should not preclude the possibility that species with more pointed mesocones, such as *Isidorella newcombi* or *Helisoma anceps*, do not also subsist mainly by scraping rather than cutting. Although the lateral tooth cusps of such species are pointed, the angles of the cusps are not acute. Such widely angular cusps may be better suited for scraping from uneven hard surfaces than more blunt-edged radular cusps.

The marginal teeth presumably function only (? or mainly) to catch torn pieces of food that have been rasped loose by the lateral teeth. Therefore, the type of food a snail eats and its shape after being rasped loose probably have some bearing on the morphology of the marginal teeth, and that might account for the differences seen in the marginal teeth between, e.g., *Bulinus* and *Planorbella, Isidorella* and *Helisoma*, or between *Gyraulus* and the other species.

Perhaps it is worthwhile noting here the contrasting habitats of *Camptoceras cosmeta* and

Bayardella johni: the former when collected were adhering to plant debris (mainly sticks) in a shallow roadside ditch, whereas the latter were found only on rocks in rivers. While both species are about the same size, and the central and marginal teeth of both are very similar, *B. johni* is characterized by a huge lateral-tooth mesocone. Such a peculiarity obviously has a relationship to the habitat/diet of this riverine snail.

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POLYMORPHISME CHROMOSOMIQUE ET NOMBRE DIPLOÏDE DANS UNE POPULATION D'*ISOGNOMON ALATUS* (BIVALVIA: ISOGNOMONIDAE)

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RÉSUMÉ

Les caractéristiques chromosomiques d'une population d'*Isognomon alatus*, originaire de l'île de Jaina, dans la région de Campêche, au Mexique, ont été analysées et comparées à celles des populations de même espèce provenant de Floride et de Veracruz. Les spécimens de Campêche présentent 26 paires de chromosomes, comparés à ceux trouvés antérieurement en Floride et à Veracruz, qui eux, comptent 28 paires. Les 26 paires de chromosomes de la population de Campêche sont réparties de la façon suivante: cinq paires métacentriques, six de type sub-métacentrique et deux de type acrocentrique, tandis que la population de Floride compte cinq paires métacentriques et neuf paires sub-métacentriques, et que celle de Veracruz révèle quatre paires métacentriques, sept paires sub-métacentriques et trois acrocentriques. Ces différences caryotypiques proviennent sans nul doute de la séparation géographique des diverses populations et des conditions dans lesquelles elles vivent dans leur environnement respectif.

ABSTRACT

Chromosome characteristics of an *Isognomon alatus* population from Jaina Island, Campeche, Mexico, have been analysed and compared to populations of the same species from Florida and Veracruz. The Campeche specimens had 26 pairs of chromosomes, compared to 28 pairs found previously in Florida and Veracruz populations. The Campeche population has five metacentric, six sub-metacentric and two acrocentric chromosomes, whereas the other populations had five metacentric pairs and nine sub-metacentric pairs for the population from Florida, and four metacentric, seven sub-metacentric and three acrocentric pairs for the population from Veracruz. These karyotypic differences may have resulted from the geographic separation of the populations and their adaptation to different enrironmental conditions.

INTRODUCTION

Des études chromosomiques, orientées vers la cytotaxonomie de quelques mollusques d'importance économique, originaires des côtes mexicaines, ont été encouragées, il y a quelques années, par l'Université Nationale Autonome du Mexique, particulièrement en ce qui concerne les espèces de la famille des Ostreidae (Rodríguez-Romero et al., 1978, 1979a,b; Rodríguez-Romero, 1981), Mytilidae (Diupotex-Chong et al., 1978) et Isognomonidae (Rodríguez-Romero et al., 1979c; Díaz y López, 1980).

L'intérêt des études cytogénétiques chez les mollusques bivalves concerne les problèmes taxonomiques, phylogénétiques, d'évolution et d'hybridation (Ahmed & Sparks, 1967; Ahmed, 1973; Stiles & Longwell, 1973; Longwell, 1976). Les problèmes taxonomiques sont importants puisqu'il est difficile d'identifier ces mollusques.

En particulier, la famille des Ostreidae provoqua des controverses (Menzel, 1968). Des études prospectives de la faune malacologique du Golfe du Mexique (Abbott, 1974) indiquent que le genre *Isognomon* présente trois espèces différentes: *I. alatus* Gmelin 1791, *I. radiatus* Anton 1839, et *I. bicolor* C.B. Adams 1845, dont chacune possède des caractéristiques d'une valeur taxonomique définie. Les principales références pour la taxonomie sont données par les particularités des coquilles; celles-ci se trouvent soumises a un vaste changement du milieu aquatique, attribué à de nombreuses causes (Hynd, 1955).

FIG. 1. Vues d'*Isognomon alatus*. A, Externe; B, interne.

Même si *Isognomon alatus* (Fig. 1) représente l'espèce la plus étudiée de la famille des Isognomonidae, juste quelques travaux relatifs à l'anatomie et l'écologie sont connus (Yonge, 1968; Siung, 1980). Quant aux études chromosomiques, Wada (1978), Rodríguez-Romero et al. (1979a,b,c) et Díaz y López (1980) ont effectué des recherches de type caryologique dans les populations de Veracruz et Floride; d'après ces travaux, le nombre diploïde et la morphologie chromosomique de cette espèce sont maintenant connus.

La comparaison des caryotypes de ces populations a reflété des différences intéressantes, relatives à la dynamique adaptative des chromosomes de cette espèce.

Le but de notre recherche est de fournir les résultats de l'étude chromosomique d'une population de *Isognomon alatus*, localisée sur les côtes du nord de l'état de Campêche (Mexique), en soulignant le nombre et le polymorphisme chromosomique.

MATÉRIEL ET MÉTHODES

Soixante douze spécimens, en provenance de l'île de Jaina (Campêche, Mexique), ont été traités pour

obtenir les chromosomes des cellules mitotiques et méiotiques; le traitement a été effectué par une technique d'égouttement et séchage à l'air, en modifiant légèrement la technique de Kligerman & Bloom (1977).

Les champs chromosomiques mitotiques et méiotiques ont été soumis à une analyse statistique d'après Levan et al. (1964) et Al-Aish (1969).

Les coquilles des spécimens deja travaillés ont été placés dans la collection malacologique qui se trouve au Laboratoire de Malacologie de l'Institut des Sciences de la Mer et de Limnologie à l'Université Nationale Autonome du Mexique (référence no. 7).

RÉSULTATS

Méiose

Les champs chromosomiques des cellules méiotiques analysées ont indiqué la présence de 13 complexes bivalents; on n'a trouvé ni hétéropycnose négative ni hétéromorphisme chromosomique qui indiqueraient la présence de chromosomes sexuels. Les chromosomes méiotiques en zygonème présentaient une complèmentation tout au long du corps chromosomique de chacune des paires homologues.

Mitose

Sur la base de la morphologie chromosomique, et principalement d'après la position du centromère, les chromosomes qui composent le caryotype ont été classés en: métacentriques, les paires 1, 2, 3, 5 et 6; sub-métacentriques, les paires 4, 7, 8, 9, 11 et 13; et sub-télocentriques, les paires 10 et 12 (Figs. 2, 3).

Bien que l'analyse n'ait pas été effectuée dans tous les champs, des constrictions secondaires et la présence de satellites étaient évidentes, au moins dans deux des paires chromosomiques les plus grandes.

DISCUSSION ET CONCLUSIONS

La morphologie des coquilles d'*Isognomon alatus*, originaires de Jaina, présente des aspects d'un grand intérêt, à cause de la variabilité de cette espèce, ce que Abbott (1974) ne mentionne pas dans sa description. D'après Abbott cette espèce se caractérise par des valves minces, assez comprimées et variables, en forme de roue, d'une longueur de 8 cm, avec 8-12 dents à la charnière, disposées perpendiculairement à la marge dorsale des valves. Les valves sont de couleur gris-brunâtre ou noire.

Or, les organismes de la Lagune de la Mancha, Veracruz, présentent tout à fait les caractéristiques mentionnées, tandis que les exemplaires de l'île de Jaina sont différents et correspondent à la description morphologique donnée par Siung (1980) d'une population de Jamaïque. Les principales différences sont: coloration brunâtre et rougeâtre, longueur de 12 cm, aproximativement, qui augmente irrégulièrement chez les organismes adultes; ces valves présentent des extensions dans leur marge postérieure. Le nombre de dents de la charnière se situe entre cinq et 13.

De même, les études cytogénétiques, réalisées dans cette espèce montrent des variations. Les résultats des recherches faites par Wada (1978), concernant le nombre diploïde et les caractéristiques chromosomiques générales d'*Isognomon alatus* de Floride, correspondent à un nombre chromosomique diploïde de 28, c'est-à-dire, 14 paires homologues, parmi lesquelles cinq sont métacentriques et les autres sub-métacentriques. D'autre part, Rodríguez-Romero et al. (1979c) et Díaz y López (1980), en étudiant les populations de la Lagune de la Mancha, Veracruz, indiquent le même nombre diploïde, mais prouvent la présence de quatre paires métacentriques, sept sub-métacentriques, une sub-télocentrique et deux acrocentriques.

Il est difficile de ranger les chromosomes des organismes étudiés à l'île de Jaina en paires homologues à cause de leur variabilité morphologique. La comparaison des caryotypes de

FIG. 2. Chromosomes mitotiques d'*Isognomon alatus* de l'île de Jaina, Campêche, Mexique; 2n = 26.

FIG. 3. Caryotype d'*Isognomon alatus* de l'île de Jaina, Campêche, Mexique; 2n = 26.

ces organismes met en évidence des différences en ce qui concerne la morphologie chromosomique et le nombre diploïde, 2n = 26. La différenciation du caryotype a été notée en deux paires acrocentriques d'*Isognomon alatus*, originaire des côtes de Floride, alors que celui de *I. alatus*, originaire des côtes de Veracruz, présente un changement dans une des paires chromosomiques; on en conclut que cette paire pourrait être sub-télocentrique ou acrocentrique. Dans les organismes originaires des côtes mexicaines, les chromosomes acrocentriques ont été détectés dans les paires les plus petites.

La comparaison des compléments chromosomiques de ces bivalves montre une différence

TABLE 1. Résultats de l'analyse statistique des mensurations des chromosomes d'un caryotype mitotique de 2n = 26 d'*Isognomon alatus* de l'île de Jaina, Campêche, Mexique.

Chromosomes	P	Q	P + Q	Longueur relative $\frac{P+q}{\text{Long C Hap.}}$ (1000)	Indice Centromérique $\frac{p}{p+q}$ (100)	$\frac{P}{q}$ Relation des bras	Différence	Classification
1	11.000	14.500	25.500	116.795	43.137	1.316	1.371	m
2	10.694	11.583	22.277	102.033	42.004	1.083	0.398	m
3	9.222	11.250	20.472	93.766	45.046	1.219	0.980	m
4	5.361	13.500	18.861	86.387	28.423	2.518	4.314	sm
5	8.444	10.389	18.833	86.259	44.834	1.230	1.031	m
6	6.681	10.930	17.611	80.662	37.936	1.636	2.409	m
7	4.889	11.111	16.000	73.283	30.556	2.272	3.887	sm
8	3.861	11.028	14.889	68.195	25.931	2.856	4.813	sm
9	4.375	9.680	14.055	64.375	31.127	2.213	3.773	sm
10	3.028	11.014	14.042	64.315	21.563	3.637	5.686	st
11	4.083	9.042	13.125	60.115	31.104	2.214	3.777	sm
12	2.889	9.472	12.361	56.616	23.371	3.278	5.324	st
13	3.250	7.055	10.305	47.199	31.538	2.170	3.621	sm

Long. C. Hap. = 218.331 1000.000

p = bras court
q = bras long
m = métacentrique
sm = submétacentrique
st = subtélocentrique
t = télocentrique

dans une paire chromosomique, puisque le nombre diploïde est 26 (Figs. 3, 4). En ce qui concerne la morphologie, la présence de chromosomes métacentriques, sub-métacentriques et acrocentriques a été prouvée; les derniers se trouvaient dans les paires les plus petites (Table 1).

S'appuyant sur le fait que les différentes populations de l'espèce *Isognomon alatus*, en provenance de Floride et de l'État de Veracruz, présentent un nombre diploïde de 2n = 28, des chromosomes acrocentriques et sub-télocentriques, White (1951) en déduit que ces mollusques ne présentent pas une haute stabilité caryotypique comme par exemple les ostréides.

Cette hypothèse suggère l'existence d'un polymorphisme chromosomique et, en même

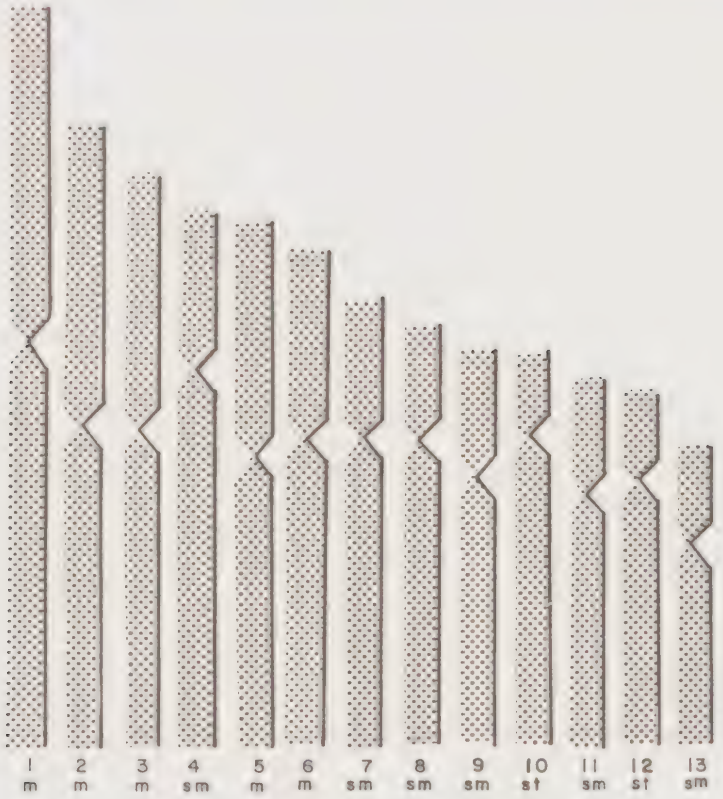

FIG. 4. Idéogramme d'*Isognomon alatus* de l'île de Jaina, Campêche, Mexique.

temps, une différence dans le nombre diploïde; celui-ci pourrait être en relation avec les conditions de milieux où ces populations prospèrent après isolement géographique.

REMERCIEMENT

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THE PRESENCE OF MURAMIC ACID IN THE LIPIDIC FRACTION EXTRACTED FROM MOLLUSCA. – Muramic acid is an acidic sugar derivative, recognizable by the presence of both carboxyl and glycosidic functions; it may be regarded as D(-)-lactic acid and N-acetyl glucosamine joined by an ether linkage. Muramic acid is a common constituent of bacterial (Gram +) walls (Cummins & Harris, 1954; Strange & Powell, 1954; Strange & Dark, 1956). It is easily obtained by extraction and acid hydrolysis (6N HCl at 100°C) following the procedure of Strange & Kent (1959). As far as we know, this compound has never been reported previously to occur in animals.

During extraction of polar lipids from the nervous ganglia of two gastropods (*Murex trunculus* Linnaeus and *Helix pomatia* Linnaeus) (Bolognani et al., 1981b), we observed negative tests for sialic acid and sialoglycolipids, while qualitative tests for muramic acid proved positive. Quantitative analyses to evaluate the concentration of this compound were therefore undertaken on nerve ganglia and on the digestive gland of these gastropods.

Materials and methods. The nervous ganglia of the perioesophageal ring of *Helix pomatia* and *Murex trunculus* were dissected from the surrounding tissues, frozen at -20°C and homogenized in chloroform-methanol (2:1 parts by volume), following the Folch-Suzuki procedure (Folch et al., 1957; Lees et al., 1959; Suzuki, 1976), as reported by Brunngraber et al. (1976). Digestive glands dissected from *H. pomatia* and *M. trunculus* also were submitted to the same procedure. The extracts were centrifuged at 10,000 x g x 10 min and the supernatants were collected. The solid sediment was extracted again with 10 ml chloroform-methanol (1:2 parts by volume) and 0.5 ml water and centrifuged at 10,000 x g x 10 min. The sedimented material was discarded, and the supernatants were pooled and stirred with 10 ml chloroform and 8 ml 0.88% KCl aqueous solution in order to partition glycolipids. The aqueous phase and chloroform (organic) phase were separated at 400 x g x 20 min. After washing the organic phase twice with 17.5 ml of chloroform-methanol-0.88% KCl (3:48:47 parts by volume), the two phases were separated again by centrifugation at 400 x g x 20 min. The aqueous phases were finally collected and dialyzed against distilled water until they gave negative chloride tests. The aqueous phases were tested as previously described (Bolognani et al., 1981a). The same phases were also tested by the colorimetric procedure for muramic acid following Hadzija (1974). Thin-layer chromatography (on 0.25 mm precoated silica-gel plates by E. Merck) before and after acid hydrolysis (6N HCl 24h at 100°C) was carried out on the concentrated aqueous phase in order to separate muramic acid-containing fractions from glycoconjugates. The solvent was n-propanol:H_2O:NH_3 (7:3:1 parts by volume). Pure muramic acid was tested simultaneously as a control by the above procedures; iodine vapours, anisaldehyde and Ehrlich's reagents were used to demonstrate it on the plates.

Results and Discussion. The aqueous phase of the nervous ganglia of *Murex trunculus* tested for muramic acid reacted positively to p-hydroxydiphenyle. The muramic acid concentration reached 1 mg/g of

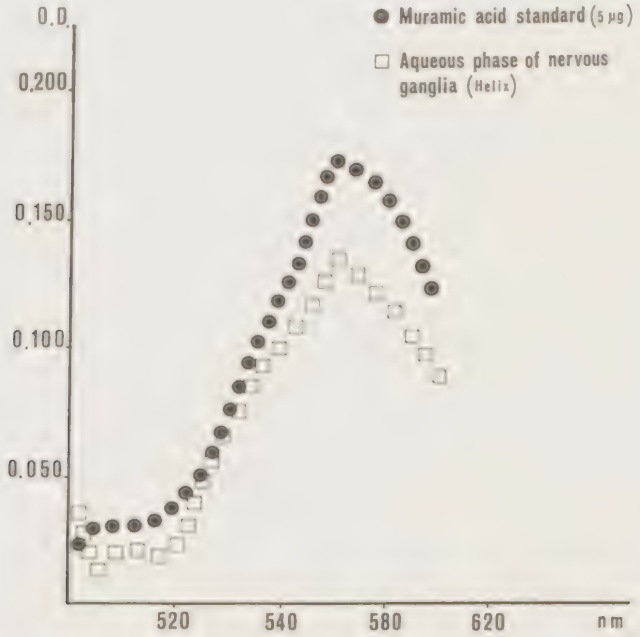

FIG. 1. Absorption spectra of the muramic acid standard and the aqueous phase of the nervous ganglia of *Helix pomatia*.

fresh tissue. Absorption spectra of colorimetric tests carried out on the muramic acid standard and on the aqueous phase of the nervous ganglia are shown in Fig. 1.

The aqueous phases from the digestive glands of *Murex trunculus* and *Helix pomatia* also were positive for muramic acid according to Hadzija (1974). The concentration of muramic acid in the digestive gland is around 250 μg/g of fresh tissue. The absorption spectra of both extracts are similar to that of a standard muramic acid solution (see Fig. 1). The muramic acid concentration is higher in the nerve tissue than in the digestive gland.

Our knowledge of the function of muramic acid is limited to an awareness that in bacteria it is bound to peptide derivatives (muramil-peptides) and it is involved in membrane structure (Martin, 1966). It has not yet been ascertained whether muramic acid in the above gastropods is located in the membranes (Bolognani et al., 1981b). It certainly can be extracted from the aqueous phase after the partition of polar lipids in the same way as some polar glycolipids. It is, however, remarkable that gangliosides appear to be the only glycolipids that are not present in the Mollusca (Araki et al., 1980; Bolognani et al., 1981a, b).

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SIPHONAL AUTOTOMY IN *SOLEN CORNEUS* (BIVALVIA: SOLENOIDEA) FROM HONG KONG. – Autotomy in the Mollusca was reviewed by Stasek (1967). Very few bivalves exhibit autotomy, a trait which is generally restricted to the Pectinoidea [autotomy of the defensive tentacles of *Lima* and *Limaria* is a good example[(Gilmour, 1963, 1967; Morton, 1979) and to *Solecurtus* and *Solen* in the Tellinoidea and Solenoidea, respectively. Both break off their siphons in response, generally, to fish predation (Smith, in Atkins, 1937). Species of *Galeomma* (Leptonoidea) also autotomise defensive papillae on the reflected mantle (Morton, 1973). Annandale (1916), Ricketts & Calvin (1952), Pohlo (1963) and Stasek (1967) have reported upon autotomy in various species of *Solen*, but only Ghosh (1916) has examined the siphons histologically. Ghosh suggested that autotomy in *S. fonesi* Dunker is the result of contraction of radial muscles interconnecting the inner and outer epithelia of the siphons. This description is incomplete, however, and a detailed examination of the siphons and mechanism of autotomy in *Solen* has not hitherto been undertaken. Conversely, Gilmour (1967) has provided a clear account of the histology and mechanism of autotomy of the tentacles of *Lima*, and this study of *S. corneus* Lamarck complements that work.

The Chinese species of the Solenidae have been revised by Tchang & Hwang (1964). Specimens of *Solen corneus* were obtained from the extensive mud flats of Deep Bay in the northwestern quadrat of the New Territories of Hong Kong. Material for sectioning was fixed in Bouins fluid. Serial transverse and longitudinal sections of the siphons were cut at 6 μm and alternate slides were stained in either Ehrlich's haematoxylin and eosin or Masson's trichrome.

The siphons of *Solen corneus* are fused, this involving inner and middle folds, and are thus of Type B (Yonge, 1957, 1982). In an adult (of about 7 cm shell length), the intact siphons comprise about 20 annulations (Fig. 1). The apical crown of the intact siphons has a characteristic arrangement of papillae (Fig. 2). The crown comprises an external ring of 24 large papillae, 12 around each of the two siphons. Rays of dark pigment border each papilla of only the exhalant siphon. Otherwise, the orifice of the exhalant aperture is naked. The orifice of the inhalant aperture, however, comprises a primary ring of six large, club-tipped, inwardly directed, primary papillae. Interspersing these are six more, similarly club-tipped, inwardly directed, but smaller, secondary papillae. These and the primary papillae are interspersed by 12 simple, outwardly directed, smaller tertiary papillae. Rays of dark pigment flank each of these. Autotomy of the distal siphonal annulations shows, as demonstrated for *S. rosaceus* Carpenter and *S. sicarius* Gould by Pohlo (1963) and Stasek (1967), respectively, that each more proximal segment has an incipient, complete set of papillae buds, both those developed externally (the ring of 24 tentacles around the apical circumference of both siphons) and the apertural crown of the inhalant. The size of these buds progressively declines in the more proximal annulations.

In transverse section, it can be seen that the siphons have a characteristic structure. Grossly (Fig. 3A), each siphon possesses six large nerves extending to the tip and located between units of a central block of longitudinal muscles. Two large blood vessels occur between the two siphons. In more detail (Fig. 3B), the siphonal wall comprises (from the outside in): 1, an outer epithelium; 2, a thick zone of sparsely packed circular muscles; 3, a large central block of longitudinal muscles; 4, a further zone of circular muscles; 5, a narrow zone of longitudinal muscle blocks interspersed between which are large numbers of single-celled, eosinophilic, subepithelial gland cells staining red in Masson's trichrome; 6, a final narrow zone of circular muscles; and, finally, 7, the inner epithelium. Inner and outer epithelia are cross-connected by radial muscles, which also divide longitudinal muscles into discrete blocks.

In longitudinal section (Fig. 4), the same structure is revealed, but at the nodes between segments more detail of their union is revealed. Both the inner and outer epithelia are here sharply indented. The distal end of each annulation is marked, externally, by a single or double fold of epithelial cells containing dark pigment granules. Beneath this occurs the external papilla. Internally, the section shows the inner epithelium, underlain in every segment by the gland cells. At the demarcation line, or fracture zone, between annulations, the central nerve is pinched and but a few of the longitudinal muscles cross a zone (some 20-30 μm thick) of lightly staining connective tissue.

Gilmour (1967) has shown for *Lima hians* (Gmelin) that each annulation of the tentacle comprises a hydrostatically discrete unit, linked to one another by septa with pores to effect hydrostatic changes in the various segments. Such a system is necessary because the tentacles are used also in swimming. Autotomy of the tentacles is brought about by an increase in the diameter of the segment proximal to the septum, while that of the segment distal to the septum is decreased. Increase in diameter is accomplished by longitudinal muscle contraction, a decrease by contraction of the radial muscles. The tentacle breaks along the line of weakness between the two connective tissue sheets of the septum, contraction of the longitudinal muscles assisting in tearing the sheets apart. An acrid mucus also is produced to deter predators. The siphons of *Solen corneus*, first, do not possess the capacious haemocoel of the *Lima* tentacles. Second, the region between annulations does not comprise a distinct septum with a pore. Third, however, gland cells are present beneath the inner epithelium. The siphons of *S. marginatus* can be made to autotomise by electrical stimulation of the visceral ganglia (Faussek (1897), in Riggenbach (1903)) and in *S. rosaceus* by rough handling (Ricketts & Calvin, 1952). It thus seems clear that a nervously controlled interraction between the contractions of the longitudinal, circular and radial muscles of *S. corneus* might be responsible for autotomy of the siphonal segments. Stasek (1967) remarks, however, that the distal segment of the siphons of *S. sicarius* can be separated easily with forceps. This is true also of *S. corneus*, and probably under normal conditions the siphonal segments of *Solen* would simply be broken off when, for example, bitten by a fish. Separation is thus by the tearing of a weak band of connective tissue, with only the nerves being more tenacious (Stasek, 1967). At the same time, subepithelial glands may discharge a (possibly) noxious mucus to either deter further attacks (though presumably the remainder of the siphons will have been retracted between the shell borders) or to coat the wounded tip of the new apical segment. In every way, therefore, autotomy of the siphonal segments of *S. corneus* is simple as compared with the complex process that occurs in *Lima*. In the latter, however, structural complexity may result from the swimming function of the tentacles rather than from the process of autotomy.

Voucher specimens of *Solen corneus* have been deposited in the Museum of Zoology, The University of Michigan (UMMZ 250292). Thanks are due to Dr. Noel Morris, Department of Palaeontology, British Museum (Natural History), for confirming the identity of *S. corneus* and to Mr. H.C. Leung, University of Hong Kong, for histological assistance.

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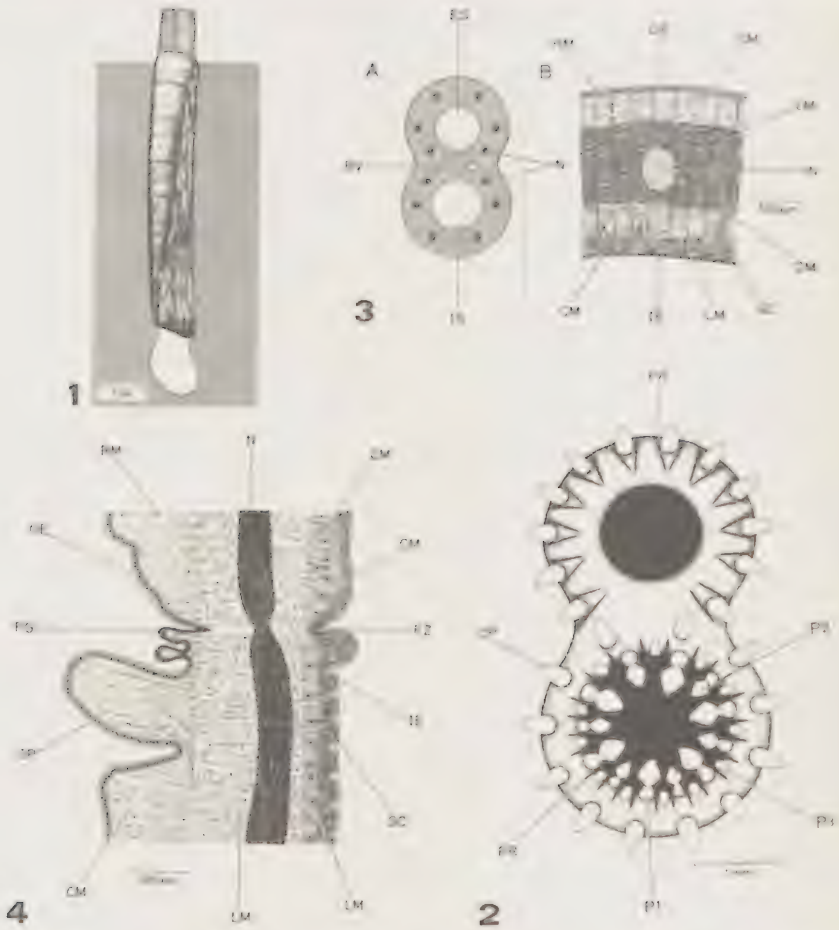

FIG. 1. *Solen corneus*. The animal in its natural position in the mud, with annulated siphons extended. FIG. 2. *S. corneus*. The siphons as seen from the posterior aspect. The exhalant siphon is dorsal. FIG. 3. *S. corneus*. A, A diagrammatic section through the fused siphons; B, detail of a transverse section through part of the siphonal wall. FIG. 4. *S. corneus*. A longitudinal section through the point of union of two annulations of the inhalant siphon.

Abbreviations: BV = blood vessel; CM = circular muscle; ES = exhalant siphon; FZ = fracture zone; GC = gland cell; IE = inner epithelium; IS = inhalant siphon; LM = longitudinal muscle; N = nerve; OE = outer epithelium; OP = outer papilla; P1 = primary papilla; P2 = secondary papilla; P3 = tertiary papilla; PG = pigment granules; PR = pigment ray; RM = radial muscle fibers.

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THE FRESHWATER MUSSELS (PELECYPODA: UNIONIDAE) OF THE UPPER TITTABAWASSEE RIVER DRAINAGE, MICHIGAN. – Many of the river drainages in Michigan have been intensively surveyed for freshwater mussels, especially those in the southern half of the lower peninsula (e.g., van der Schalie, 1936, 1938, 1948, 1970; Strayer, 1979, 1980). However, certain watersheds, such as the upper Tittabawassee River (UTR) drainage, have not been thoroughly investigated. This study, believed to be the first comprehensive investigation of the UTR drainage, will add substantially to the current knowledge of the unionid fauna of the lower peninsula of Michigan. Additionally, since it is thought that the freshwater mussel fauna of the UTR drainage is derived from the Grand River fauna by means of a post-glacial confluence (van der Schalie, 1941), this investigation may be useful in the interpretation of zoogeographic patterns.

Study area. The UTR drainage, one of the major tributaries of the Saginaw River which empties into Lake Huron, drains approximately 2.36 x 10^3 km^2 of Clare, Gladwin, Midland, Ogemaw and Roscommon counties in east central lower Michigan. The main rivers constituting the system are the Cedar, Tobacco and Tittabawassee, which can be characterized as predominantly low gradient hardwater streams. Non-impounded stream widths ranged from 1-30 m, with mean depths varying between 0.2-1.5 m. Soils within the watershed are mainly sand with some clay loam overburdened with sand. Land use in this sparsely populated region is approximately 62% forest and 34% agricultural.

Methods. From 1979 through 1981, freshwater mussels were collected from the UTR drainage. Fifty sites were thoroughly investigated. Reported below are the 28 sites from which freshwater mussels were taken. Live specimens as well as dead shells were handpicked from the shallows with the aid of waterscopes. Recently dead valves were scored as living specimens in Table 1. Identifications were made according to Burch (1975). Reference specimens are housed at the University of Michigan, Museum of Zoology.

Collecting stations. 1) Howard Cr. at Ruhle Rd. (S8,R2W,T15N; Midland Co.); 2) Tittabawassee R. below Sanford dam (S24,R1W,T15N; Midland Co.); 3) Tittabawassee R. below E. Edenville dam (S36,R1W, T17N; Gladwin Co.); 4) Tobacco R. below W. Edenville dam (S35,R1W,T17N; Gladwin Co.); 5) S. branch Tobacco R. at Beaver Rd. (S30,R4W,T17N; Clare Co.); 6) Mid. branch Tobacco R. at McCollouch Rd. (S2,R2W,T17N; Gladwin Co.); 7) Mid. branch Tobacco R. at Bard Rd. (S5,R2W,T17N; Gladwin Co.); 8) Tobacco R. above Beaverton dam, Beaverton (S12,R2W,T17N; Gladwin Co.); 9) Cedar R. at Howard Rd. (S30,R1W,T18N; Gladwin Co.); 10) Cedar R. at Hwy. M-61 (S1,R2W,T18N; Gladwin Co.); 11) Cedar R. at Oberlin Rd. (S35,R2W,T19N; Gladwin Co.); 12) Cedar R. below Chappel dam (S27,R2W,T19N; Gladwin Co.); 13) Tributary draining Lake Contos (S28,R2W,T19N; Gladwin Co.); 14) N. branch Cedar R. at Meredith Grade (S15,R2W,T20N; Gladwin Co.); 15) Sugar R. at Hwy. M-30 (S13,R1W,T19N; Gladwin Co.); 16) S. branch Little Sugar R. at McClure-Cemetery Rd. (S2,R1W,T19N; Gladwin Co.); 17) S. branch Little Sugar R. at Hockaday Rd. (S9,R1W,T19N; Gladwin Co.); 18) S. branch Little Sugar R. at Butman Rd. (S7, R1W,T19N; Gladwin Co.); 19) W. branch Tittabawassee R. at Hwy. M-30 (S33,R1E,T20N; Gladwin Co.); 20) W. branch Tittabawassee R. at Sugar River Rd. (S14,R1W,T20N; Gladwin Co.); 21) Mid. branch Tittabawassee R. at Bensch Rd. (S7,R2E,T20N; Gladwin Co.); 22) Mid. branch Tittabawassee R. at Beardsly Rd. (S26,R1E,T21N; Ogemaw Co.); 23) Mid. branch Tittabawassee R. at Ehinger Rd. (S22,R1E,T21N; Ogemaw Co.); 24) E. branch Tittabawassee R. at Greenwood Rd. (S29,R2E,T21N; Ogemaw Co.); 25) E. branch Tittabawassee R. at Wickes Rd. (S30,R2E,T21N; Ogemaw Co.); 26) Fish Cr. at Deer Rd. (S17,R2E, T18N; Gladwin Co.); 27) Molasses R. at Hwy. M-61 (S7,R2E,T18N; Gladwin Co.); 28) Molasses R. at Mosquito Alley (S32,R2E,T19N; Gladwin Co.).

Results and Discussion. Fourteen species of freshwater mussels were collected from the UTR drainage over a two-year period (Table 1). Of these, *Ptychobranchus fasciolare* was found only as badly eroded dead shells. It is likely that this species is no longer extant in the drainage. Additionally, due to the preponderance of highly eroded, adult valves and the corresponding paucity of living individuals found in our survey, we conclude that *Elliptio dilatata* is on the decline in the UTR. Two species, *Anodonta grandis* and *Actinonaias ellipsiformis*, were among the most abundant and widely distributed mussels in this river system.

In a paper on the rare and endangered mollusk species of the Great Lakes region, van der Schalie (1975) stated that *Actinonaias ellipsiformis* has been devastated by various human activities. Subsequently, the Michigan Department of Natural Resources (Michigan Department of Natural Resources, 1976) listed this species as threatened in the state. However, our investigation confirms the existence of many, widely distributed, actively recruiting populations of *A. ellipsiformis* in the UTR drainage. It is probable that other viable populations of *A. ellipsiformis* still exist in relatively undisturbed headwater streams within the distribution described by van der Schalie & van der Schalie (1963).

Although it generally is accepted that the unionid fauna of the Saginaw River drainage is derived from the fauna of the Grand River of west central lower Michigan (van der Schalie, 1941), the faunal list presented by van der Schalie does not place *Ptychobranchus fasciolare* in the Grand River. This is due to the fact that *P. fasciolare* is primarily a Mississippian faunal element that is thought to have migrated northward via the Wabash-Maumee confluence, entering Lake Erie and the streams tributary to that lake in southeastern Michigan during post-glacial times (Goodrich & van der Schalie, 1944). The presence of *P. fasciolare* in the UTR requires another explanation. Either a post-glacial confluence occurred between the Saginaw River drainage and a southeastern Michigan stream or *P. fasciolare* dispersed via Lake Erie to Lake Huron and subsequently into the Saginaw River drainage.

The present zoogeographic distribution of *Lampsilis fasciola* and *Actinonaias ellipsiformis* does not corroborate the hypothesis that faunal exchange has occurred between the Saginaw River drainage and the

TABLE 1. List of species found at each station in the upper Tittabawassee River drainage, Michigan (collected 1979-81).

Mussel species	Station number																									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Actinonaias ellipsiformis (Conrad)	A					C	R			A	C	C			A	A	R	C			A	A	A		R		C	A
Alasmidonta calceolus (Lea)	R				A	R						R				C		C			C	R	R	R				R
Alasmidonta marginata Say				R°											R						R°							
Anodonta grandis Say	A		R	A	R			A	R°			A	A		R	A	C	A								C		A
Anodonta imbecilis Say								A				A																
Anodontoides ferussacianus (Lea)									R°			R			R	R		C	R°	R°	R	C	R	R				
Elliptio dilatata Rafinesque		R°		R°		R°		R													R							
Fusconaia flava Rafinesque				R°				C				R																
Lampsilis ovata (Say)		R		C								C			R													
Lampsilis radiata siliquoidea (Barnes)		R	R	A				A		R	R	A	C	R°	R	C	R	C									C	A
Lasmigona complanata (Barnes)								C																				
Lasmigona compressa (Lea)	R				R				R°	R		C			R	R		R			R	R	C		R	R		C
Ptychobranchus fasciolare (Rafinesque)		R°																										
Strophitus undulatus (Say)				R																								

°Found only as dead eroded shells.

Abbreviations: A (abundant) = >5 clams/man hr; C (common) = 1-5 clams/man hr, R (rare) = <1 clam/man hr.

streams of southeastern Michigan. Although suitable habitat exists for both species in each drainage, *L. fasciola* remains confined to southeastern Michigan streams and *A. ellipsiformis* remains excluded from these same streams (van der Schalie, 1941). However, since *Ptychobranchus fasciolare* has been found in Lake Erie and Lake St. Clair (Goodrich & van der Schalie, 1932), it is likely that *P. fasciolare* reached the Saginaw River drainage by way of Lake Huron.

One of the most striking characteristics of the UTR drainage is its abundance of impoundments created by power dams. Two prominent adverse effects of impoundment on freshwater mussel populations are increased siltation and the modification of potential host fish faunas (Fuller, 1974). It is also evident that dams isolate mussel populations by restricting the fish potentiated phoresis of larval clams, thereby eliminating the possible recolonization of locally decimated populations. *Ptychobranchus fasciolare* and *Elliptio dilatata* may be cases in point regarding this particular phenomenon in the UTR. If, in fact, these two species are extant in Lake Huron, the dams on the UTR preclude the possible reestablishment of these mussels due to their obvious impediment to upstream fish migration.

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LAMPSILIS REEVEIANA AND *LAMPSILIS STRECKERI* (BIVALVIA: UNIONACEA): SOME CLARIFICATION. – Classification of *Lampsilis reeveiana* (Lea, 1852) (junior synonyms: *Unio breviculus* Call and *L. brittsi* Simpson) has been confused since its original description when Lea published the collector's address (Dr. J. Hale, Alexandria, Louisiana) rather than the type locality: "White River, Arkansas" penciled inside the allotype USNM 85025a[1] (Gordon, 1980; Johnson, 1980). Simpson (1914) listed it as both *L. (L.) brevicula* and *L. (Eurynia) reeveiana*. Utterback (1916) considered it *E. (Micromya)*, now known as *Villosa*, although he described a *Lampsilis*' anatomy for *E. (M.) brevicula* and treated *L. reeveiana* as a separate species. Ortmann (1918) placed the species (as *brevicula*) in *Lampsilis*, while Frierson (1927) relegated it to the subgenus *Ligumia* under *Lampsilis*. Recently, Burch (1975) and Johnson (1980) retained it in *Villosa*.

A major diagnostic criterion for *Lampsilis* is the presence of a mantle flap anterior to the branchial siphon in females. This is an extension of the inner lobe of the mantle edge and occurs rudimentarily in males. In *Villosa*, this area of the female is developed as a series of variably shaped and spaced papillae and is also rudimentary in males (Ortmann, 1912). Females of both genera exhibit pulsating contractions of this region (flapping behavior) prior to glochidial discharge. Utterback (1916) noted a mantle flap in his anatomical description of *Eurynia (Micromya) brevicula*. Ortmann (1918, as *brevicula*) and Kraemer (1970, as *brevicula brittsi*) confirmed the presence of the mantle flap and noted a close anatomical relationship to *L. radiata siliquoidea* (Barnes). Kraemer (1970) also noted a behavioral repertoire close to this species. Mantle flap morphology and spawning behavior are summarized in Table 1 for *reeveiana* and two *Lampsilis* species commonly sympatric with it. From the above, it is evident that *reeveiana* is a *Lampsilis*.

TABLE 1. Morphology of mantle flaps and spawning behavior for living *Lampsilis reeveiana*, *L. radiata siliquoidea* and *L. ventricosa*.

Characteristic	*L. reeveiana*	*L. radiata siliquoidea*	*L. ventricosa*
Eyespots	Inconspicuous, usually apparent on outside of flap only	Inconspicuous, apparent on outside and inside of flap	Conspicuous, apparent on outside of flap only
Flap pigmentation	Uniform, dark gray on outer surface	Variegated, many pigment spots on outer surface	Uniform gray on outer surface
	Conspicuous, large pigment spot near "tail" of each mantle flap	Conspicuous pigment spot near the base of "tail" of each mantle flap	No pigment spot
"Tail" of the mantle flap	5-10 long papillae attached to "tail" provide flaps with flaring appearance	10-20 long papillae attached to "tail" and its base provide flap with fringed, flaring appearance	Narrow, tapered "tail"
Maximal rate of flapping	17-20 pulses per minute	17-20 pulses per minute	Up to 3 pulses per second
Typical angle of orientation to substrate during flapping behavior	45° or less	45° or less	Commonly up to 90°
Environmental stimuli which evoke modifications of flapping behavior	Mechanical disturbance of substrate or water column	Mechanical disturbance of substrate or water column	Increments or decrements of low intensity light

Lampsilis reeveiana is endemic to north and south slopes of the Ozark Plateaus (Gordon, 1980; Gordon et al., 1980; Johnson, 1980). This includes the Osage, Gasconade and Meramec river systems of the north slope and the White River basin of the south slope. It is not present in the west slope drainages of the Illinois River or tributaries of the Neosho River (Gordon & Brown, 1981), although it appears to be replaced in these streams by *L. rafinesqueana* Frierson. Restriction of *L. reeveiana* to the Ozark Plateaus suggests a relict species (Gordon, 1981). This is supported by the geologic age of the uplift and endemism (Gordon et al., 1980). Except for *L. radiata siliquoidea*, there appears to be no morphologically similar, extant *Lampsilis* north of the southern limit of glaciation or within the Tennessee-Cumberland basin. Burch (1975), Gordon (1980), Gordon et al. (1980) and Johnson (1980) noted an association between *L. reeveiana* and *L. streckeri* Frierson. Johnson (1980) synonymized *L. streckeri* as *Villosa vibex* (Conrad) and, as such, contrasted its shell to that of *L. reeveiana* (as *Villosa*). Any relationship between *L. reeveiana* and southeastern *Villosa*, as suggested above, would seem improbable. However, if *streckeri* is a *Lampsilis*, representing some convergence conchologically with *V. vibex*, there is an interesting relationship between the distribution of *L. reeveiana* and other southwestern *Lampsilis* (Gordon et al., 1980).

Johnson (1980) considered the similarity in raying as a criterion for synonymizing *Lampsilis streckeri* as *Villosa vibex*. While *V. vibex* may exhibit broken raying, *L. streckeri* and *L. reeveiana* may develop rays with an inverted chevron pattern. *L. streckeri* exhibits a variably low posterior pseudocardinal similar to *V. vibex*; however, the dentition (particularly pseudocardinals) is not as lamellar. Nacre is grayish with some bluish iridescence posteriorly and tends to be blotched with brown, while *V. vibex* is bluish-white to pink or purple, more iridescent, and tends not to be blotched. Overall, the shell of *L. streckeri* is more similar to *L. reeveiana* than to *V. vibex*. In fact, the types of *L. streckeri* were identified originally as "*Unio reeveiana* Lea" (by W.A. Marsh, labels with UMMZ 91075) as were the Onion Creek specimens (Frierson, 1927; see below). Johnson (1980) seemed to imply that Frierson's types were collected together with *V. vibex* at the same locality. Frierson probably meant they were found cataloged with specimens of *V. vibex*.

Lampsilis streckeri is known only from two localities: Little Red River of the White River system, Arkansas, and Onion Creek, Travis County, Texas, in the Edwards Plateau region. Strecker (1931) listed a third locality (Salado Creek, Bell County, Texas) but the validity of this collection is unknown. These represent upland habitat with rocky

[1] USNM = U.S. National Museum of Natural History; UMMZ = University of Michigan Museum of Zoology.

FIG. 1. Geographical range of *Lampsilis reeveiana, L. streckeri* and *L. bracteata* with regard to the Ozarks and Edwards Highlands, limit of maximum glaciation, and limit of Cretaceous embayment. 1, Interior Highlands; a, Ozark Plateaus; b, Ouachita Mountains. 2, Edwards Highlands; a, Edwards Plateau; b, Central Texas Highland.
– - – = Southern limit of glaciation; – – – = limit of Cretaceous-Tertiary embayments by the Gulf of Mexico; ▲= *L. reeveiana*; ● = *L. streckeri*; ■ = *L. bracteata*. (Open symbols represent the restricted type localities.)

substrates and fairly fast flowing water. Preferred habitat of *Villosa vibex* is mud or soft sand with accumulations of plant detritus (Johnson, 1972), which also implies slower moving water. The upland habitat of *L. streckeri* is in distinct contrast to that of *V. vibex* in the coastal plain. These distributions may be related to habitat modification from the Cretaceous-Tertiary embayments of the Gulf of Mexico (Gordon et al., 1980). *V. vibex* has never been reported from Arkansas (Gordon, 1980; Gordon et al., 1980), and Neck (pers. comm.) believes *Villosa* in Texas is limited to *V. lienosa* (Conrad). It seems probable that *L. streckeri* and *V. vibex* are not conspecific.

An apparent preference for geologic uplifts (Fig. 1) exists. *Lampsilis reeveiana* is endemic to the Ozarks while *L. streckeri* exhibits a disjunct distribution between the Ozarks and Edwards Highlands. Thus, a potential relationship between *L. reeveiana* and southwestern *Lampsilis* (e.g., *L. bracteata* (Gould), type locality here restricted to Llano River, Llano, Llano County, Texas) is possible. There are some morphological similarities among the shells of these species. However, without access to an anatomy of the animal, the true systematic position of *L. streckeri* will never be known. Frierson's (1927) types were collected by Elwood Pleas in 1872 (labels with UMMZ 91075), while the Onion Creek specimens date from Askew (in Singley, 1893; Strecker, 1931). No other confirmed specimens have been collected since. The type locality of *L. streckeri*, here restricted to Little Red River, Clinton, Van Buren County, Arkansas (from Pleas' labels), is now inundated by Greer's Ferry Reservoir, which incorporates hypolimnetic discharge. Neck (pers. comm.) has never seen *L. streckeri* or *Villosa vibex* in Onion Creek, although he has found *L. bracteata*. *L. streckeri* may be extinct.

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COMPARATIVE RESPIRATION IN TWO SPECIES OF FRESHWATER UNIONID MUSSELS (BIVALVIA). – The purpose of the following investigation is to determine and compare the respiratory rates of two species of unionid mussels, *Elliptio complanata* (Solander) and *Anodonta grandis* Say, from the same lake. Both species are commonly found in lakes and rivers of the Canadian St. Lawrence drainage system. They frequently occur together and have been reported on all types of bottom, varying from soft mud or clay to coarse gravel (Clarke, 1973). However, in the lake where the study was undertaken, intensive surveys over two seasons indicated that *E. complanata* was restricted to sandy bottom, whereas *A. grandis* occurred on substrata composed of mud or clay mixed with vegetative debris.

Animals were collected from depths of 0.5 to 2 m in Lac Yvan, a small, eutrophic lake in the Laurentians, 50 km to the north of Montreal, Canada. They were transferred to aquaria within 12 h and were subsequently held at appropriate water temperatures (5, 10, 15, 20 and 25°C) for 48 h prior to the commencement of determination of rates of oxygen consumption. Oxygen consumption rates were measured with a Beckman Field Lab Oxygen Analyser. Rates were determined on individual animals in chambers of known volume immersed in a constant temperature bath at the appropriate temperature. Control chambers contained no animals.

Two types of chambers were used. In experiments designed to determine rate of oxygen consumption with decreasing oxygen tension, water was circulated by means of a small rotary pump through a plastic incubation vessel (2.5 l). An oxygen probe was inserted in the system and continuous records of oxygen consumption were maintained over periods of 6-12 h. Four specimens (1-4 g dry tissue weight) of each species were placed, in turn, in the respirometer and allowed to exhaust the available oxygen. Temperatures were maintained at 20-22°C in each experiment.

In experiments designed to measure oxygen consumption at different temperatures, 700 ml glass jars with snap caps were used. Because the experimental animals were actively pumping water in their vessels throughout the experiments, no additional stirring device was required. Incubation times were 1 h in all cases, and oxygen concentrations were measured at the beginning and end of the experiment. Between 15 and 20 individuals were tested at each temperature. After removal from the respirometers, the animals were removed from their shells, dried to a constant weight and reweighed on a Mettler H 10 W balance.

Fig. 1 shows the rates of oxygen consumption with decreasing oxygen concentration of four individuals each of *Anodonta grandis* and *Elliptio complanata* in the flow-through respirometer. In both species, rates of oxygen uptake were relatively constant between concentrations of 9 to about 1 mg O_2/l. Below concentrations of 1 mg/l the rates in all individuals dropped sharply.

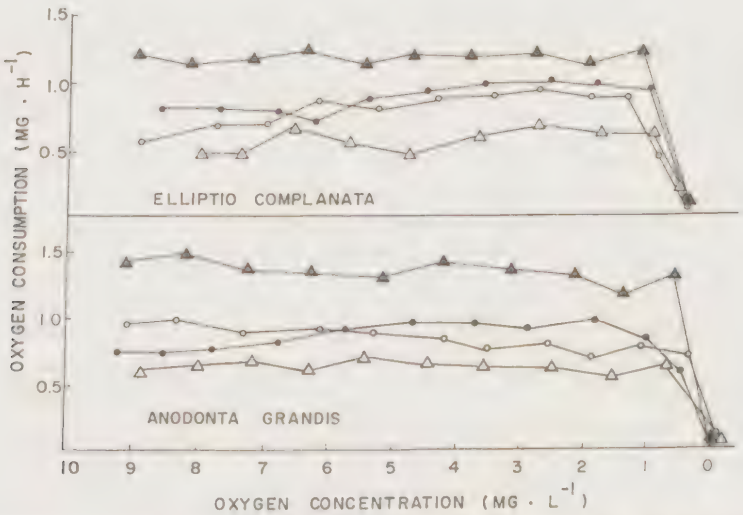

FIG. 1. Oxygen consumption of *Elliptio complanata* and *Anodonta grandis* with declining oxygen tension.

In Fig. 2, the regressions of oxygen consumption on dry body weight are plotted for *Elliptio complanata* and *Anodonta grandis*, respectively, between 5 and 25°C. Although rates of oxygen consumption commonly are expressed as weight-specific rates and regressions on size show an inverse relationship, Kenney (1982) has demonstrated that spurious self-correlations arise when two parameters that are used in a linear regression analysis have a common term. For this reason, comparisons of respiration rates at different temperatures are based simply on the relationship between oxygen consumption and size of the animals. There were no significant intraspecific differences between slopes of the lines ($P = 0.05$).

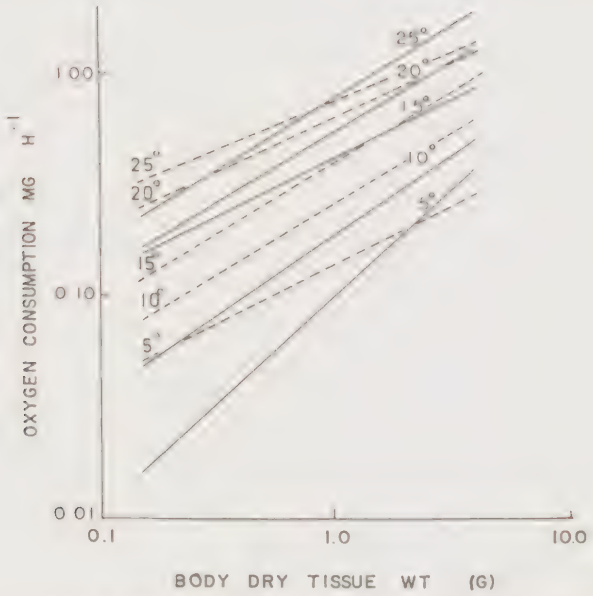

FIG. 2. Oxygen consumption of *Elliptio complanata* (solid lines) and *Anodonta grandis* (dashed lines) at different temperatures.

Analyses of covariance showed that there were significant differences (P = 0.01) in ordinal values of the regression lines and thus respiration rates increased with increasing temperatures between 5 and 25°C in both species. Analysis of covariance tests also showed that there were statistically significant differences (P = 0.01) in ordinal values between the two species (F values, 16.91 and 18.32) at 5 and 10°C, but no interspecific differences at temperatures higher than 10°C.

From the records of the decrease in oxygen concentration of the water in the flow-through incubator, it is evident that both species of mussels are regulators and oxygen uptake remained constant over a wide range of oxygen tensions. This is typical of most aquatic poikilotherms (Prosser & Brown, 1961). Only when oxygen concentration fell below 1 mg/l was there any significant decrease in the rate of uptake. If, as Evermann & Clark (1918) suggested, mussels burrow deeply in the substratum in winter, then toleration of very low oxygen tensions must be required for several months. However, Fuller (1975), who has reviewed the literature on responses of freshwater clams and mussels to low levels of oxygen, concluded that there is a great deal of variability in their capacity to respire.

Both species showed increasing rates of oxygen uptake between 5 and 25°C. Again, this is typical of poikilotherms (Prosser & Brown, 1961) and has been demonstrated in Unionidae (Lukacsovias & Salanki, 1964). Only at 5 and 10°C were there any interspecific differences in respiration rates. *Elliptio complanata* had significantly lower rates of oxygen uptake at 5 and 10°C than had *Anodonta grandis*. This suggests that *A. grandis* is more active at lower temperatures than is *E. complanata*. It is arguable that a higher metabolic rate at low temperature would enhance its burrowing ability in the spring, when temperatures are still low and when flooding due to snow runoff might cause increased sediment deposition. Furthermore, *A. grandis* might remain more active and feed for a longer period than *E. complanata* in the spring and autumn, when water temperatures are low.

Voucher specimens have been retained in the Redpath Museum, McGill University.

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THE DATE AND AUTHORSHIP OF *BORNELLA* AND *CERATOSOMA* (NUDIBRANCHIA) AND OTHER MOLLUSCS COLLECTED DURING THE VOYAGE OF H.M.S. SAMARANG, 1843-46. – In a recent paper on the nudibranch genus *Bornella*, Bertsch (1980) has given an example of the nomenclatural complications that surround the date of publication of the molluscan reports of the Samarang Expedition by Adams & Reeve (1850) and the almost simultaneous publication of some volumes of Mrs. Gray's (1842-57) *Figures of molluscous animals . . .*, in which J.E. Gray (1850) inadvertently used names for genera and species from Adams' Samarang material for the first time. The title page of the Mollusca report (Adams & Reeve, 1850) gives the publication date as 1848, but, as Bertsch noted, the report actually appeared in three parts and the opisthobranch section (pp. 63-68) was published in August 1850. J.E. Gray used some of Adams and Reeve's manuscript names in *Figures of molluscous animals . . .*, and, as volumes 2-5 of the latter work appeared in February 1850, the Samarang names of Adams and Reeve were actually published by J. E. Gray (1850) six months earlier (Bertsch, 1980).

However, what generally has been overlooked in the literature is that, as part of Belcher's (1848) general account of the Voyage of the Samarang, Adams, who was assistant surgeon on board, included a long general account of the natural history of the countries visited, which contained two pages (pp. 494-495) on which new nudibranchs from Borneo were described in anticipation of Adams & Reeve's (1848-50) full report of the Mollusca. This 1848 publication affects previous statements on the relative priority of Adams and Reeve's and Gray's names. In the following account, the nudibranch genera *Bornella* and *Ceratosoma* are discussed.

Bornella. In the case of *Bornella*, Adams & Reeve (1850: 66) gave a full definition of the genus and attributed it to Gray, so confirming his priority. On p. 67, two species of *Bornella* are described, and on pl. 19 they are illustrated: *B. digitata* Adams & Reeve and *B. adamsii* Gray. In Gray (1850: 107) there is the entry, "9. BORNELLA. Back three tufts of simple and branched tentacula. // 1. B. Adamsii, *Gray; Adams MSS.* t. 176. f. 6." Although the reference to pl. 176 is incorrect (it appeared in vol. 2, pl. 196), the above entry and illustration are sufficient to characterise the species and the genus. The original illustration of the figure copied by Mrs. Gray appeared in Adams & Reeve (1850, pl. 19, fig. 3). As Bertsch (1980) stated, it generally is accepted that the two "species" in Adams & Reeve are in fact one and that *B. adamsii* J.E. Gray has priority (six months) over *B. digitata*. However, this situation is affected by Adams' (1848) report on Borneo in which he wrote (p. 494), "Among new and interesting forms of . . . Nudibranchiata, may be mentioned two new species of *Dendronotus*, one of which (*D. stellifer*, Adams and Reeve) is of a pale flesh colour, marked with undulating vertical vermilion lines, freely anastomosing towards the foot, and the veil overhanging the head provided with a star-shaped tentacular appendage on each side. The other species of this curiously-shaped genus (*D. tenellus*, Adams and Reeve) adheres like the former to floating *Fuci*; crawls pretty briskly, and swims, when detached, by lateral inflexions of the body." This passage refers to the two species of *Bornella*, *B. digitata* and *B. adamsii*, reported later by Adams & Reeve (1850). *B. digitata* is described as "adhering to floating *Fuci*: it crawls briskly and when detached swims by lateral inflexions of the body," which is the same observation published by Adams (1848) for *D. tenellus*. *B. adamsii* is the same as *D. stellifer*. Adams & Reeve (1850) in their comments on *Bornella* said they "resemble *Dendronotus* of Alder and Hancock." Of the two earlier names, *D. stellifer* Adams & Reeve is accompanied by a clear description, while *D. tenellus* is not. However, they obviously are both the same as the two *Bornella* species, and, as those two are considered conspecific, so too must be *D. stellifer* and *D. tenellus*. As *D. stellifer* appears first and is accompanied by a good description, I, as the "first reviser" under the International Code of Zoological Nomenclature, designate *D. stellifer* to have priority over *D. tenellus*.

The clarification of *Bornella*, as proposed by Bertsch (1980), again must be amended. While the genus name *Bornella* is still attributable to J.E. Gray (1850), the correct name for the type species must change from *B. adamsii* Gray 1850 to *B. stellifer* (Adams & Reeve in Adams, 1848), and *B. tenellus* (Adams & Reeve in Adams, 1848) must join *B. adamsii* Gray 1850 and *B. digitata* Adams & Reeve 1850 in the already lengthy list of synonyms noted by Bertsch (1980).

Ceratosoma. Most authors have followed Rochebrune (1895) in attributing the genus *Ceratosoma* to Adams & Reeve (1850: 67-68) and accepting *C. cornigerum*, which they illustrated (pl. 19, fig. 5) as the type species by monotypy. However, as with *Bornella*, Gray listed *Ceratosoma* in an earlier work (1850, vol. 4, p. 105) as follows: "21. CERATOSOMA. Back produced behind. // 1. C. trilobata. Doris t. *Gray*, t. 67. f. 14. Doris, *Adams MSS* t. 214 f. 7." Although this description is brief, it is sufficient to establish Gray's authorship of the name. The one species listed, *C. trilobata*, is the type by monotypy. This species first appeared in print on an unnumbered plate of molluscs in the *Encyclopaedia Metropolitana* bearing a subscription stating that the plate was first published in 1827. Below the illustration is "*Doris trilobata* India." The plate again appears in a complete set of the encyclopaedia republished in 1845. Until other evidence is found, the correct citation for the type species should be *C. trilobata* (Gray 1827). Unfortunately, no characters are given to distinguish the species other than the original figure and another figure published later (M.E. Gray, 1842, pl. 67, fig. 14) as *D. trilobata*. Although the species is unrecognisable from the figure, the characteristic shape of the body shows unquestionably that *D. trilobata* is congeneric with *C. cornigerum*, the species on which subsequent authors have based their understanding of the genus. As there is no confusion concerning the concept of the genus group *Ceratosoma*, there is no need to ask the International Commission on Zoological Nomenclature to suppress *C. trilobata* and validate *C. cornigerum* as the type species.

The nomenclatural situation is complicated by Gray's (1850) citation of the type species. He listed two pictures appearing in *Figures of molluscous animals . . .* . The first, pl. 67, fig. 14, appears in vol. 1, 1842, and is listed as *Doris trilobata* (original). The second, pl. 214, fig. 7, appears in vol. 3 (Feb. 1850) and on p. 42 is listed as "*Doris trifida*, Gray, Adams' drawing. Borneo." It is a copy of Adams & Reeve's illustration (1850, pl. 19, fig. 5) of *Ceratosoma cornigerum*. The name, *D. trifida*, apparently is an error by Gray for *D. trilobata*, because later (Gray, 1857) he again listed both illustrations under *C. trilobata*.

There is no way to determine whether the animals represented in the two figures are conspecific, for only the latter, *Ceratosoma cornigerum*, gives sufficient colour details to enable a specific identification to be made. Although Gray's name, *C. trifida*, would appear to be an error, there is no direct evidence to show this. The name *C. trifida* would, therefore, predate *C. cornigerum* by a few months. However, in Adams (1848: 494) we find: "Among the Doridídae, the *Polycera cornigera* (Adams and Reeve) is one of the most beautiful of the family, the body being of pale straw colour, beautifully marked with bright vermilion, which covers entirely the dorsal portion, and descends

in numerous vandykes towards the foot; there is a row of bright ultramarine spots on the anterior tubercle and another row of the same colour extending across the top of the head." This clearly refers to *C. cornigerum* and, as it was published two years before Gray, it removes any need to seriously consider the validity of *C. trifida*.

The nomenclatural position then is as follows: (a) *Ceratosoma* J.E. Gray in M.E. Gray, Feb. 1850, type species (by monotypy): *Doris trilobata* J.E. Gray 1827; (b) *Ceratosoma cornigerum* (Adams & Reeve in Adams, 1848) = *Polycera cornigera* Adams & Reeve in Adams, 1848: 494 = *Doris trifida* J.E. Gray in M.E. Gray, Feb. 1850: 42, pl. 214, fig. 7 = *Ceratosoma cornigerum* Adams & Reeve, Aug. 1850: 68, pl. 19, fig. 5.

Discussion. While nomenclatural decisions, as outlined above, may appear unnecessarily pedantic, until these early complications are sorted out, no semblance of stability can be achieved. It is unfortunate that nudibranch taxonomy was dominated by Bergh for so many years. His attitude to nomenclatural problems and earlier names was to ignore them if he felt his own name was more appropriate. As O'Donoghue (1929) has written concerning Bergh, "This author had a curiously cavalier manner of sweeping aside names, species and genera, that has resulted in a deal of confusion in subsequent work in the Nudibranchiata." Since Bergh was such a prolific worker, the names he chose to use have tended to dominate contemporaneous and subsequent literature.

In the above two cases, no great change in current usage is involved. The widely used name *Bornella digitata* recently has been replaced by the little used name *B. adamsii* by Bertsch (1980), and to replace this with *B. stellifer* hardly can be said to interfere with stability. By following the rules of priority (as in the *Bornella* example), the well-used name *Ceratosoma cornigerum* can be conserved, rather than be replaced with *C. trifida*. Although initially it may seem simpler to assume that *Doris trilobata* and *C. cornigerum* are conspecific, there is no available evidence to show this. Also, as *D. trilobata* is a considerably older name (1827, not 1850 as quoted by Thompson, 1975), it would mean replacing a well-used name for a recognisable entity with an unused name based on something unrecognisable at the species level. The specific identity of *C. trilobata*, the type species of the genus, remains unknown, but the characteristic shape of tropical members of the genus *Ceratosoma* is clear even in preserved specimens, so no confusion is likely to arise from the impossibility of recognising the type species.

In general, Adams' account (1848) contains many references to molluscs, including interesting observations on the living animals, which often appear to be the first published observations of the species involved. As the work is arranged geographically, notes on molluscs are scattered widely through the text. Adams must have assumed that the formal descriptions of new taxa would appear simultaneously, so there is no easy way of identifying what are in fact first references to names in mollusc groups with which I am not familiar.

Bertsch (1980) has illustrated the importance of referring to Gray (1850) when determining the authorship and date of Adams & Reeve's (1850) Samarang material. It is suggested here that the general account of the zoology of the countries visited by the Samarang (Adams, 1848) also should be checked for inadvertent first descriptions.

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I.M. Likharev, Ya. I. Starobogatov

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I.I. Shuvalova

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PREFACE

These abstracts are from reports to the Sixth Meeting on the Investigation of Molluscs, which was organized by the Malacological Committee of the Scientific Council on "Biological Bases for the Use, Reconstruction and Protection of Animals". The meeting was held 7-9 February 1979 in the Zoological Institute of the Academy of Sciences of the U.S.S.R. (Leningrad).

The abstracts of the previous (Fifth) Meeting were published in *Malacological Review*, 1978, Vol. 11, pp. 63-156. There were 149 abstracts in the Russian language proceedings of the Sixth Meeting on the Investigation of Molluscs. Only 51 of these abstracts are presented here in English – those abstracts which are thought to be of special interest for foreign colleagues and which have not been published later in other scientific journals.

All inquiries concerning this Meeting should be addressed to the Malacological Committee, Zoological Institute, Academy of Sciences of the U.S.S.R., Universitetskaja Embankment I, Leningrad B-34, U.S.S.R.

Ya. I. Starobogatov

The titles of the papers presented at the Sixth Meeting on the Investigation of Molluscs are listed below. English language abstracts of those marked with an asterisk are printed on the pages which follow (pp. 111-149).

PROGRAM

*Agarova, I.I. Some aspects of the linear growth of bivalve molluscs in a population of *Cerastoderma edule belgicum*.

*Akramowski, N.N. The history of formation of the land and freshwater molluscan fauna in the eastern part of the Transcaucasian upland.

*Alexandrov, D.A. & Sergievsky, S.O. A variant of sympatric speciation in snails.

Alimov, A.F. Functional-ecological features of freshwater bivalve populations.

*Almuhambetowa, S. Pupilloidea of the Talass Alatau Mountains.

*Alyakrinskaya, I.O. Adaptations of mollusc embryos to nutrition and respiration.

*Amitrov, O.V. The marine Paleogene gastropods from southern USSR (comparative analysis of assemblages).

Antipova, T.V. Zoogeographical characteristics of the Bivalvia of the Barents Sea and the Kara Sea.

*Antonov, P.I. The possibility of age determination in *Dreissena polymorpha* (Pallas) by the structure of the septal surface.

Arakelova, E.S. The influence of reduced oxygen content on the metabolic rate of prosobranch snails.

Arsan, O.M. Dependency of the activity of respiratory enzymes in the tissues of bivalve molluscs on phosphorus content.

Babak, E.V. The history of the family Dreissenidae in the Pliocene-Quaternary Euxinic basin.

*Barskov, I.S. Life-forms and ecogenesis of cephalopods in the Paleozoic.

Beer, S.A. & Lurje, A.A. Radioisotopic marking of freshwater molluscs.

Beljakova, I.V. Freshwater molluscs of Kazakhstan as intermediate hosts of Trematoda.

Berjoskina, G.V., Kiseljova, L.N. & Konstantinova, T.S. Dependence of calcium and magnesium content in the Lymnaeidae shell on species and age of mollusks and on hydrochemical regime of ponds.

Bondarchuk, L.G., Doroshenko, O.V., Stadnychenko, A.P. & Dudko, E.V. On the changes in the vitamin balance in bodies of freshwater gastropod mollusks infected with parthenites of trematodes.

*Bregman, J.E. Morphology and population structure of the bivalve *Patinopecten yessoensis* Jay of the Soviet Far East.

*Bykov, A.N. & Dubinina, I.S. Some peculiarities of larval development of the family Enoploteuthidae in the central-east Atlantic.

Cheremnov, A.D. Results of a study of freshwater molluscs of the Upper Jenisei drainage.

Chernogorenko, M.I. & Kurandina, D.P. Investigations on the digenean trematode fauna of Prosobranchia from the Lower Dniepr collected over a period of several years.

*Chistikov, S.D. Phylogenetic relations of scaphopods.

*Denysenko, S.G. Some aspects of the ecology and growth of the scallop *Chlamys islandica* (Müller) in the Barents Sea.

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Egorova, E.N. Zoogeographical composition of the malacofauna in the Davis Sea (East Antarctica).

Ezhkova, N.S. Biology and morphology of the cuttlefish *Sepia elegans* Orb. off the seacoast of North-West Africa.

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*Filippova, J.A. & Juchov, V.L. Peculiarities of the Teuthofauna in Antarctic waters.

Gadjieva, S.B. The food value of molluscs of the western part of the southern Caspian.

*Gaevskaya, A.V. The principal results and perspectives of a study of the Atlantic cephalopod helminthofauna.

*Galaktionov, K.V. The seasonal dynamics of invasion of *Littorina saxatilis* by the parthenite *Microphallus pygmaeus* (Levinsen, 1881) (Trematoda: Microphallidae) in Yarnyshnaya Bay (eastern Murman).

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*Galperina, G.E. Periodicity of growth and reproduction in the Caspian bivalve *Didacna trigonoides*.

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*Järvekülg, A.A. The ecology of the bivalves in the eastern part of the Baltic Sea.
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*Krasnenkov, R.V. First results of research on Pliocene and Pleistocene land molluscs in the basin of the Don.
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Kruglov, N.D., Starovogatov, Y.I. & Schmakov, V.T. Morphological, genetic and biochemical analysis of *Lymnaea stagnalis* var. *producta* and *Lymnaea stagnalis* var. *stagnalis*.
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*Lubarskaja, O.D. & Galimova, D.N. A study of bivalves of the family Pisidiidae and their parasites in Tatar, ASSR.
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ABSTRACTS

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FORMATION OF METAMERIC ORGANS DURING THE ONTOGENESIS OF CHITONS

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Abstract

Peculiarities in the organization of chitons always have been used in solving the problems of the origin and evolution of molluscs. A discovery of Recent monoplacophorans has helped in making a detailed comparison of metamery in different classes, and as a result an old idea of the origin of molluscs from polymeric ancestors has been revived (Pelseneer, 1899; Lemche, 1959; Lemche & Wingetrand, 1959; Fretter & Graham, 1962). Supporters of the hypothesis of the primary americ nature of molluscs, however, give forcible arguments in its defense (Yonge, 1947). A study of the development of metameric organs of chitons will enable us to approach the solving of this complex problem. We studied formation of some metameric organs (organs of respiration, shell plates, nerve commissures) in *Tonicella marmorea* (Fabricius), *Ischnochiton* sp. and *Lepidopleurus* sp.

Hunter & Brown (1965) in their special investigation noted that the branchial system of chitons in its definitive state is characterized by some fundamental peculiarities. First, the number of gills in chitons constantly increases, being in correlation with weight and age of molluscs. Second, the number of gills in the right and left pallial grooves can vary significantly; this asymmetry is intensified due to the circumstance that the degree of differentiation of some pairs of gills varies in wide ranges. We have confirmed the observations of the above authors. It has been noted as well that in many individuals (including very young forms at the formation of the first 10 gills) the organs of respiration are not located metamerically but alternate; thus, a distinct branchiomere is lacking in them. Of greatest interest is a formation of primary ctenidia; in the studied species, one or (seldom) two pairs of ctenidia are formed in ontogenesis. These primary gills have a constant localisation near an excretory pore and always form a distinct branchiomere. The formation of the following respiratory organs occurs after a long period of "rest" when, however, a differentiation of the shell and of most internal organs is carried out. These relations correspond, apparently, to the initial structure of primary molluscs which had a diplomeric organization with two pairs of ctenidia and auricles of the heart (Minichev & Starobogatov, 1975). In the evolutionary line leading directly to chitons, a reduction of a pair of ctenidia took place; this pair is traced as an atavistic character in the development only of some individuals of recent chitons. All the other organs of respiration of chitons are new formations (adaptive gills).

Ways and succession of formation of shell plates in chitons are different (Kowalevsky, 1883; Heath, 1899; Hammarsten & Runnström, 1925; Smith, 1966). The development of *Tonicella marmorea* and *Lepidopleurus* sp., which we studied, is characterized by a number of peculiarities. First, plates are not formed simultaneously, in a definite succession; time intervals in the formation of the plates can vary in different individuals. Second, at first only one plate, usually the sixth, is formed (seldom the fifth and sixth); all the other plates are formed in front of or behind these primary plates. Third, each plate is differentiated from two separated centers which dilate to the center and periphery of the notum; the inorganic part of the plates is formed by means of fusion of numerous calcareous scales. These facts suggest two suppositions: 1) it is very possible that the very first plates correspond to the primary plates of ancestors of chitons, in which they covered the area of the double set of mantle organs; 2) two-center formation of plates enables us to compare shells of chitons and bivalves.

The nervous system of *Tonicella* is formed as brain and one pair of longitudinal trunks with diffuse plexus between them; pleuro-visceral trunks appear in ontogenesis later. Differentiation and metamerisation of commissures are accomplished at first in the area of formation of renopericardial complexes (in the region of the sixth shell plate) that confirms once again the hypothesis of monomeric (or diplomeric) nature of primary forms.

Taking into consideration peculiarities of formation of metameric organs in Recent forms as well as paleontological data in the evolution of chitons, it is possible to distinguish the following stages corresponding in the taxonomic respect to three distinct subclasses: Archaeoloricata Minichev & Sirenko, Paleoloricata Bergenhayn 1955 and Neoloricata Bergenhayn 1955.

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SOME PROBLEMS IN THE SYSTEMATICS AND PHYLOGENY OF THE SUBORDER PUPILLINA (GASTROPODA: GEOPHILA)

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Abstract

Most ancient reliable members of Pupillina found in the Upper Cretaceous-Paleocene are represented by reliably identified species of Recent genera (*Azeca, Cochlicopa, Vertigo, Orcula, Vallonia, Acanthinula*). Therefore, the suborder appeared much earlier, not later than the middle Mesozoic, though there were known Permian-Carboniferous genera and species (Dendropupidae) belonging, apparently, to this suborder.

The early evolution of Pupillina was carried out in a close connection with adaptations to different habitats in forest biotopes that affected, first of all, sizes of animals. If the shell height of ancestral forms was 5 to 10 mm (most archaic Recent groups have just such sizes, on the average), then the appearance of taxa, which are composed of both small and large species, should be associated with two main types of forest biotopes: litter and trunks. Adaptation to the life in a layer of fallen leaves led to a reduction of sizes of animals and to the appearance of Pupillidae and Vertiginidae; the formation of relatively large Buliminidae is connected with the life on trunks of trees. The reduction of sizes was achieved not only by the reduction proper with a preservation of proportions of the shell but also by the acquirement of the ability to breed before the shell achieves the definitive state. This resulted in an early cessation of growth of shells and in a formation of microhelicoid forms (Strobilopsidae, Valloniidae).

The principal characters of the shell, which are of phylogenetic significance, were analyzed in a paper devoted to the system and phylogeny (Schileyko, 1979). That is why here an analysis of anatomical characters may be in order. The most characteristic feature of the reproductive system of Pupillina is the primary availability of a complex penial appendix. Naturally, the presence or absence of this appendix is given a great taxonomic significance. So, in respect to Buliminidae, it became a tradition to refer any species without an appendix to Chondrulinae. As a result, such dissimilar genera as *Chondrula, Senaridenta* and *Cyrenaeus* are referred to Chondrulinae, without paying attention to the fact that *Senaridenta* practically does not differ from *Multidentula* and *Cyrenaeus* hardly differs from *Paramastus*. When dissecting "*Jaminia*" *pupoides* (Krynicki) from different localities, Hudec (1972) found that a penial appendix was missing in individuals collected near Stepanakert. In this connection, he described a new species and referred it not only to the genus *Chondrula* but also to its nominative subgenus. All conchological characters isolate quite distinctly from all other Buliminidae a group of species which earlier was assigned to the genus *Jaminia* (*Buliminus pupoides, B. lamelliferus* Rossmaessler, *B. nachicevanjensis* (Hudec), *B. angustior* Retowski, *B. phasianus* Mousson, *B. ovularis* Olivier). These characters are so close in all these forms that without knowing their anatomy they can be taken for one species; it should be noted that all prominent conchologists regarded them as synonyms or very close species. It should be emphasized that the shell in this case is specialized and can be characterized by many features; this reduces the possibility of occasional convergence to a minimum. The decisive character which unites all these forms is the presence of a closed papilla of the penis in the above forms, while in all other Buliminidae except Middle Asiatic *Chondrulopsina* such a papilla is missing.

The genus *Cyrenaeus* should be mentioned in this respect. The genus *Paramastus* (Bulimininae) is characterized by the presence of a penial appendix. Brandt (1958), when investigating species from North Africa, established that the appendix was missing in them. Due to this, Heller (1971) separated them into a distinct genus, *Cyrenaeus*, and assigned the new genus to Chondrulinae, though eastern Asiatic *Paramastus* and North African *Cyrenaeus* possess a complex of very similar characters. This suggests that the reduction of the penial appendix in Buliminidae occurred at least three times (*Chondrula, Senaridenta, Cyrenaeus*). Therefore, we can distinguish Chondrulinae as a distinct subfamily with only the genus *Chondrula* with its subgenera; this genus, however, is so close to other Eninae that this step is hardly expedient.

A similar situation is observed in Vertiginidae. Thiele (1931) separated the tribes Vertigineae and Nesopupeae. The anatomy of most Nesopupeae is unknown, and in *Nesopupa* there is a penial appendix which is missing in *Vertigo* and close genera. It should be noted that the tribes have no other distinguishing characters. Nevertheless, Zilch (1959-60) made the next step and the tribes are raised to subfamilial rank, though diagnoses of these subfamilies almost coincide. Scanty material on the anatomy of Nesopupinae does not yet allow us to give an evaluation of the subfamily as a whole, but it is clear that in this subfamily, and in the Buliminidae as well, the reduction of the appendix could take place more than once.

Let's regard this situation from the historical and ecological point of view. More archaic Buliminidae, which have a penial appendix, live up to now in forests or biotopes similar in their microconditions to forest ones. Virtually all cases of the reduction of the appendix have relevance to molluscs which began to inhabit arid treeless areas, though the appendix did not prevent them from living in steppe landscapes. In other words, all the forest groups have the appendix and among non-forest ones there are forms both having the appendix and lacking it; the transition to a new adaptive zone served as a stimulus for a reduction of the organ. The absence of the appendix points to the improvement of the process of sperm exchange.

As regards Vertiginidae, more archaic Nesopupinae auct., which have the appendix, are inhabitants of humid tropical areas; Vertigininae gravitate towards temperate zones of the northern hemisphere. It is quite possible that the absence of the appendix enabled them to occupy northern forests and to reach the northern Polar Circle: it is not by chance that the most abundant and large species *Vertigo modesta* (Say) is one of the most northern members of the family. One of the causes of a relation between the absence of the appendix and occupation of high latitudes is, apparently, of energetic nature.

Judged by the results obtained, we suggest the following family level systematics for the suborder: 1) Ceriidae; 2) Cochlicopidae; 3) Amastridae; 4) Achatinellidae; 5) Orculidae (Orculinae, Pagodulininae, Lauriinae, ?Argninae); 6) Strobilopsidae (Strobilopsinae, ?Spelaeodiscinae); 7) Vertiginidae (Gastrocoptinae, Vertigininae, Truncatellininae); 8) Chondrinidae; 9) Pupillidae; 10) Buliminidae (Retowskiinae, Eninae, Bulimininae, Pseudonapaeinae, Jaminiinae, Chondrulopsininae, Multidentulinae, Cerastuinae); 11) Valloniidae (Acanthinulinae, Valloniinae); 12) Pyramidulidae.

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TAXONOMY OF OPISTHOBRANCHIA AND PECULIARITIES OF THE EVOLUTION OF THE REPRODUCTIVE SYSTEM

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Abstract

In addition to the usual ectodermal formations (bursal, pallial, cephalopodial divisions), the reproductive system

of the Opisthobranchia has a special structural element (ootypical loop) which is formed as an invagination of the integument of the pallial cavity and produces a glandular part of the reproductive system. As a rule, all Opisthobranchia have the second spermatic reservoir, the spermatheca, which opens near the female genital orifice. In some groups, the copulatory organ is formed near the female genital opening; in the other groups, it is formed in the region of the head. In the first case, the most primitive reproductive systems consist in the ectodermal part of the pallial gonoduct, with bursa (spermatocyst) entering apically the ootypical loop. The gonoduct above the loop or at the level of its median part separates the vas deferens, which ends with a non-retractile copulatory organ (the order Acteonida). The reproductive system of lower members of the order Pleurobranchida (suborder Pleurobranchina) is formed approximately in the same way. They have a retractile copulatory organ and the bursa always opens into the pallial gonoduct above the place of its junction with the ootypical loop. In the suborder Berthellinina, the bursa and spermatheca always open as a common duct near the female orifice. In the suborder Berthelleina (considering the genus *Berthella*), a special vaginal duct, where the bursa enters, and the spermatheca split off from the ootypical loop (triauly).

Evolution of the reproductive system in the order Phyllidiida proceeded in a similar way. In the suborder Bathydoridina, the bursa is missing, there is only the spermatheca; the general structure of the reproductive system is nearly the same as in Pleurobranchina. In the suborder Cadlinina, the bursa and spermatheca open as a common duct into the female orifice; in the suborder Onchidoridina, the structure of the reproductive system is the same as in the Pleurobranchina and the spermatheca and bursa are always present. In the suborder Okadaiina, a vaginal duct splits off from the ootypical loop but the bursa and spermatheca open above the loop. In the suborder Doridina, triauly appears on account of the splitting of the vaginal duct, where the bursa and spermatheca enter, while, in the suborder Phyllidiina, the bursa opens into the pallial gonoduct and the spermatheca into the vaginal duct.

The adaptive radiation of the reproductive systems in the order Tritoniida resembles that of the above orders. It is more varied, however, and this makes us divide the order more finely than usual. Thus, we separate dendronotoids with a diaulic reproductive system into the suborder Tritoniina, but keep the forms with a triaulic reproductive system (the vaginal duct is separated) in the suborder Dendronotina. The same is true in respect to arminoids. Diaulic forms belong to the suborder Dermatobranchina and triaulic forms to the suborder Janolina. The suborder Acolidiina is characterized by a separate position of spermatic reservoirs (the bursa is above the ootypical loop, the spermatheca is near the female opening, one of the reservoirs is sometimes missing); in the suborder Flabellinina, both reservoirs open as a common duct into the female opening or near it; in the suborder Coryphellina, both reservoirs open into the gonoduct above the ootypical loop; in the suborder Glaucina, the reproductive system is triaulic and the spermatheca enters the vaginal duct. The uniform general pattern and directions of the evolution of the reproductive system speaks in favor of the belonging of these orders to one superorder.

In most forms united under the name Saccoglossa (except the bivalved opisthobranchs and *Cylindrobulla* and *Volvatella*), the copulatory organ is also situated near the female opening. The order Oxynoida is characterized by a certain shift of the ootypical loop upwards; in the suborder Lobigerina, the reproductive system is diaulic and in the suborder Oxynoina it is triaulic. The structure of the reproductive system of the order Stiligerida has the same pattern as that of Oxynoida, but the ootypical loop is not shifted upwards. The reproductive system of the suborder Caliphyllina, where diauly is observed and the ootypical loop is of usual structure, is most simple. In the diaulic reproductive system of the suborder Phyllobranchopsina, the ootypical loop is torn above the place of opening of the pallial gonoduct; in the suborder Stiligerina, the reproductive system is triaulic, but the ootypical loop is not torn; in the suborder Hermaeinina, which has the triaulic reproductive system, the ootypical loop is torn and there is one female opening instead of two as in Stiligerina. The order Polybranchiida is characterized by the bifurcating oviduct above the glandular part of the ootypical loop, the suborder Polybranchiina having a diaulic reproductive system and the suborder Elysiina having a triaulic reproductive system with a separated vaginal duct. The above groups of Saccoglossa have an albuminous gland of a special type, which is situated in the apical part of the visceral sac (apparently of renal origin) and enters the hermaphroditic duct or the beginning of the oviduct. This, together with peculiarities of the digestive system, suggests the unity of these three orders in one superorder..

Of all Opisthobranchiata in which the copulatory organ is situated in the region of the head, the reproductive system in the order Runcinida and in the suborder Diaphanina of the order Bullida is most primitive. A closed part of the reproductive system ends with a normal ootypical loop and then an open seminal groove goes to the copulatory organ. In the other suborders of the order Bullida, the loop is torn: in Bullaina, lower than the place of opening of the pallial gonoduct; in Philinoglossina, above the place of opening of the pallial gonoduct; and, in Hamineina, the ootypical loop is divided into three parts – one of them remains higher than the place of opening of the pallial gonoduct and is torn from above, the second is torn lower, and the third is torn at the opening of the pallial gonoduct (albumen gland). The structure of the reproductive systems of the orders Aplysiida and Pneumodermatida is very similar. In the suborder Phyllaplysiina of the first order, the ootypical loop is greatly shifted upwards but the reproductive system is monaulic and, in the suborder Aplysiina, it is diaulic but with a single pallial genital opening. The unity of structure and evolution of the reproductive system in the above four orders speaks in favor of their belonging to one superorder.

In the bivalved Saccoglossa and in *Cylindrobulla* and *Volvatella*, the copulatory organ is also situated in the region of the head, but the sperm passes to it along the closed vas deferens (though there is a groove) which is situated under the skin. The structure of the reproductive systems is similar in its main characters; that is why we can consider this group as a distinct order, Tamanovalvida. In the suborder Cylindrobullina, the ootypical loop is of the usual structure and the vaginal duct is not separated. In the suborder Volvatellina, the vaginal duct opens into a common female opening and is separated and, in the suborder Tamanovalvina, there is an additional duct which connects the vaginal duct with the middle of the glandular one. We do not agree that the genus *Tamanovalva* is a synonym of *Berthellinia*, and so we follow nomenclatural priority in regard to the names of the order and suborder. This latter order resembles the other groups with the copulatory organ situated in the region of the head by some characters of the reproductive system and is similar to other Saccoglossa by the structure of the digestive system. It belongs to an as yet unnamed superorder.

Systematics of the orders and suborders of Opisthobranchia is as follows: Superorder **Acteobranchia** Minichev & Starobogatov 1975 (= Phyllidioida Férussac 1822). Orders: Acteonida Minichev 1967, Pleurobranchida Deshayes

1830 (with suborders Pleurobranchina Deshayes 1830, Berthellinina Minichev & Starobogatov 1979, Berthelleina Minichev & Starobogatov 1979), Phyllidiida Férussac 1822 (with suborders Bathydoridina Minichev & Starobogatov 1979 = Gnathodoridacea Odhner 1934, Cadlinina Minichev & Starobogatov 1979, Onchidoridina Minichev & Starobogatov 1979, Okadaiina Minichev & Starobogatov 1979, Doridina Odhner 1934, Phyllidiina Férussac 1822), Tritoniida Férussac 1822 (with suborders Tritoniina Férussac 1822, Dendronotina Odhner 1936, Dermatobranchina Férussac 1822, Janolina Minichev & Starobogatov 1979, Aeolidiina Odhner 1934, Flabellinina Minichev & Starobogatov 1979, Coryphellina Minichev & Starobogatov 1979, Glaucina Minichev & Starobogatov 1979). Superorder Saccoglossa Ihering 1876 (= Polybranchioida Férussac 1822). Orders: Oxynoida Baba 1966 (with suborders Lobigerina Minichev & Starobogatov 1979, Oxynoina Baba 1966), Stiligerida Minichev & Starobogatov 1979 (with suborders Caliphyllina Minichev & Starobogatov 1979, Phyllobranchopsina Minichev & Starobogatov 1979, Stiligerina Minichev & Starobogatov 1979, Hermaeinina Minichev & Starobogatov 1979), Polybranchiida Férussac 1822 (with suborders Polybranchiina Férussac 1822, Elysiina Baba 1949). Superorder Cephalaspidea Fischer 1887 (= Bulloida Férussac 1822). Orders: Bullida Férussac 1822 (with suborders Diaphanina Minichev & Starobogatov 1975, Bullaina Férussac 1822, Philinoglossina Hoffmann 1933 = Philinina Minichev 1967, Hamineina Minichev & Starobogatov 1979), Runcinida Burn 1963, Aplysiida Franc 1968 (with suborders Phyllaphysiina Minichev & Starobogatov 1979, Aplysiina Franc 1968), Pneumodermatida Minichev & Starobogatov 1975 (with suborders Pneumodermatina Minichev & Starobogatov 1975, Laginiopsina Minichev & Starobogatov 1979 = Gymnoptera Van der Spoel 1972).

Another superorder apparently can include the order Tamanovalvida Kawaguti & Baba 1959 (with suborders Cylindrobullina Baba 1966, Volvatellina Baba 1966 and Tamanovalvina Kawaguti & Baba 1959). The systematic position of the latter order or superorder is not yet clear.

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PHYLOGENETIC RELATIONSHIPS OF THE SCAPHOPODA

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Abstract

The position of Scaphopoda within the Mollusca and the phylogenetic relationships within this class continue to be debated. The point of view that the Scaphopoda represents a little-changed branch of the primitive Xenoconchia is now receiving an ever increasing acceptance. A comparison of the Scaphopoda with the Monoplacophora and the Gastropoda gives a possibility to outline some possible homologies. Thus, captacular supports of Scaphopoda, considering their topography and the character of innervation, should be regarded as homologies of velum in *Neopilina* rather than of postoral palps as Lemche suggested. It is very possible that paired postoral appendages took part in the formation of the oral tube of Scaphopoda. The formation of the foot in the Scaphopoda proceeded, apparently, on account of protruding of the ventral wall of the body and strengthening of its musculature; initially paired and strongly dissected epipodia happened to be shifted far to the end of this new foot and turned into a collar in the order Dentaliida and into a ring of digitate appendages in some Gadilida. Such homology is confirmed by the position of statocysts and pedal ganglions, which in Dentaliida are situated in the anterior wall of the foot far from its base. In investigated members of Gadilida (*Bathoxiphus tricarinatus* (Boissevain), *Polyschides sacurai* (Kuroda & Habe), *Compressidens* sp.), however, statocysts are at the base of the foot. When comparing shells of Scaphopoda with those of Monoplacophora and Gastropoda, two possibilities should be considered: 1) the apertural edge of the shell in Gastropoda is homologous only to the aperture of Scaphopoda; this means that in Monoplacophora and Gastropoda the apical orifice was lost for the second time; in addition, such interpretation suggests that telotroch of larvae in Scaphopoda and Gastropoda are not homologous; 2) the apertural edge of the shell in Gastropoda is homologous to the aperture, abdominal suture and apical orifice of Scaphopoda. A choice of any of the hypotheses is impossible until new data appear.

The order Dentaliida has a morphological row, Dentaliinae - Laevidentaliinae - Episiphonidae (*Gadilina* and close groups). Strongly deviating Rhabdoidea separated, apparently, early from the main trunk. The genus *Plagioglypta*, from our point of view, should be excluded from the order Dentaliida. The presence of a cleft at the ventral edge of the aperture points to an incomplete confluence of mantle leaflets. The absence of longitudinal sculpture so characteristic of most primitive Dentaliida and Gadilida makes their derivation from *Plagioglypta* difficult. The latter are known as little changed from Ordovician to Upper Cretaceous, while typical Dentalioidea (*Quasidentalium*) are reported from the Carboniferous. The absence of exogastric bent from *Plagioglypta* can be regarded as a progressive character.

On this basis *Plagioglypta* should be separated into a distinct order, Plagioglyptida Chistika 1979. Diagnosis: shell is straight or nearly straight, only with rough collabral lines of growth, aperture with a long cleft or deep U-shaped incision on the abdominal side. (Presumably: two pairs of retractors, foot with a rudimentary sole, paired dissected epipodia, radula of a gadilid type, possibly with seven teeth in each row).

The order Gadilida has a compact group of genera characterized by a number of primitive characters, which should be separated into a distinct family, Entalinidae Chistikov 1979. Diagnosis: shell with longitudinal sculpture, often carinate, strongly bent at the apex. Dorsal wall is thicker than abdominal one. Aperture inclined. Shell is shortened on account of erosion of the apical end. Anterior edges of central teeth of radula bear tricuspid or trisected plates protruding forwards and upwards; they are somewhat smaller than thickened parts of teeth. Lateral teeth with three large cusps: the first upper cusp is moved backwards; between the second and third cusps there are large denticles. Genera: *Heteroschismoides, Entalinopsis, Entalina, Megaentalina* and *Bathoxiphus*. The forms close to Entalinidae may be regarded as ancestors of other Gadilida.

On the whole, the Gadilida are more adapted to burrowing and therefore are more advanced than Dentaliida. At

the same time, the radula of the former resembles that of the Docoglossa and *Neopilina*; the mantle valve is not so complex as that of Rhabdidae and Episiphonidae. The contractile foot of Gadilida could hardly develop from the muscular secondary foot of Dentaliida and digitate appendages from the collar. On the contrary, we have reasons to believe that the marginal part of the collar in Dentaliida is formed by fused filaments. The orders Dentaliida and Gadilida should be regarded as independent descendents of ancient Plagioglyptida and they developed, apparently, as far as in the Cambrian.

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THE SYSTEMATICS OF THE SUBORDER MYTILEINA (BIVALVIA)

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Abstract

Families and superfamilies united by us (Scarlato & Starobogatov, 1975; 1979) into the suborder Mytileina are considered to be distinct ones due to the structure of their ligament, dentition and shell (chevron-shaped duplivincular ligament in arcoids and quite different types in other groups). The origin of oysters from arcoids is confirmed by the presence of homologues of the promyal passage in the latter and by the presence (only in the latter) of a combination of opisthogyrate umbones with a prosodethic ligament (as in young oysters). The whole order Mytilida is characterized by an early and very complete reduction of the anterior part of the dorsal margin, accompanied by the disappearance of the anterior part of the cardinal area with anterior submarginal teeth. Thus, in arcoids, the dentition is formed on account of subumbonal and posterior submarginal teeth of actinodont dentition. The arcoids are characterized as well by the shift of umbones backwards in respect to the ligament, so amphydethic and prosodethic ligaments rearose in members of this group from the opisthodethic ligament. In addition to the duplivincular ligament with a typical chevron-shaped pattern on the ligamental area, other types of ligament are peculiar to arcoids, so a duplivincular type (mechanical analogue of multivincular one) is only the end result of the evolution, which began from a simple alivincular ligament of cyrtodontids, while the other types (prosodethic in *Litharca*; opisthodethic in mytiloids, etc.) should be regarded as lateral branches of this evolutionary row. The dentition is very diverse, too, and the transition from dentition of cyrtodont type (with anterior subumbonal and posterior submarginal teeth) to a typical arcoid one took parallel courses. All this made us review the system of families and superfamilies of the suborder. We do not consider here the systematics of genera and give only the main genera.

Mytiloidea. Mytilidae Rafinesque 1815, shell elongated anteroposteriorly: Arcuatulinae Scarlato & Starobogatov 1979, umbones noticeably behind the anterior edge, the anterior adductor large or double (Miocene-Recent: *Arcuatula, Amygdalum, Geukensia, Gregariella, Mytella, Terua*), Musculinae Iredale 1939 (Jurassic-Recent: *Musculus, Arvella, Megacrenella, Lioberus, Vilasina, Trichomusculus, Idasola*), Modiolinae Keen 1958 (Eocene-Recent: *Modiolus, Stavelia, Modiolula, Semimytilus*), Trichomyinae Scarlato & Starobogatov 1979, shell with terminal umbones and radial sculpture (Oligocene-Recent: *Trichomya, Antetrichomya*), Brachiodontinae Scarlato & Starobogatov 1979, shell triangular, sculptured, with subterminal umbones and noticeable dysodont dentition (Jurassic-Recent: *Brachiodontes, Mauricia, Mytilaster, Semimodiola*), Mytilinae (Jurassic-Recent: *Mytilus, Crenomytilus, Perumytilus, Arcomytilus*), Perninae Scarlato & Starobogatov 1979, sculptured, seldom smooth, with terminal umbones, anterior adductor only in young specimens (Miocene-Recent: *Perna, Aulacomya, Ischadium*). Crenellidae Gray 1840. Shell elongated dorsoventrally: Botulinae Scarlato & Starobogatov 1979. Shell smooth with prosogyrous umbones (Triassic-Recent: *Botula, Botulopsis, Arcoperna, Notobotula, Rhynchomytilus, Dacrydium*), Crenellinae (Cretaceous-Recent: *Crenella, Solamen*). Lithophagidae H. & A. Adams 1850: Lithophaginae, umbones subterminal (Miocene-Recent: *Lithophaga*). Adulinae Scarlato & Starobogatov 1979, umbones somewhat shifted forward from the middle (Recent: *Adula*). Septiferidae Scarlato & Starobogatov 1979, shell modioloid or mytiloid with septum where the anterior adductor is attached: Limnoperninae Scarlato & Starobogatov 1979, umbones subterminal, septum poorly developed (Recent: *Limnoperna, Fluviolanatus, Peregrinamer, Adipicola, Miridas*). Septiferinae, umbones terminal, septum well developed (Triassic-Recent: *Septifer, Ciboticola, Sinomytilus* (for diagnosis see Thiele, 1935, p. 801; type species *Dreissena crosseana* Morelet, by monotypy)).

Bathyarcoidea. Ligament opisthodethic, shifting ventrally but little with the growth of the shell. Macrodontellidae Scarlato & Starobogatov 1979, anterior teeth oblique, posterior ones horizontal (Triassic: *Macrodontella*). Postligatidae Scarlato & Starobogatov fam. nov., shell roundish, dentition of two rows of oblique short teeth; rows meet each other forming an angle under the umbones (Cretaceous: *Postligata*). Bathyarcidae Scarlato & Starobogatov 1979, anterior teeth vertical, posterior ones oblique, separated from anterior ones by a wide interval (Eocene-Recent: *Bathyarca, Bentharca, Samarca*). Lunarcidae Scarlato & Starobogatov 1979, all teeth nearly vertical, as two unequally long contiguous groups (Eocene-Recent: *Lunarca*).

Cucullaeoidea. Ligament alvicular, dentition developed. Catellidae Scarlato & Starobogatov 1979, anterior teeth oblique, posterior ones horizontal: Poteriinae Scarlato & Starobogatov 1979, shell *Barbatia*-like without dorsoventral groove (Eocene-Recent: *Poterius, Paragarammatodon*). Catellinae, shell irregularly triangular with dorsoventral groove (Triassic-Jurassic: *Catella*). Nemodontidae Scarlato & Starobogatov 1979, all teeth horizontal (Cretaceous: *Nemodon*). Cucullariidae Habe 1977, teeth short, parallel to cardinal edge, under umbone small vertical teeth present, ligament shortened (Eocene: *Cucullaria*). Cucullaeidae Steward 1936, teeth form a continuous row, anterior dorsal ends directed forward, posterior ones backwards (Jurassic-Recent: *Cucullaea*). Cunearcidae Scarlato & Starobogatov 1979, teeth vertical, as two indistinctly separated groups, marginal reinforcements of lamellar layer of the ligament parallel to cardinal edge present (Oligocene-Recent: *Cunearca*). Melaxineidae Scarlato & Starobogatov 1979, teeth as two oblique rows, anterior and posterior dorsal angles of the shell protruded behind the cardinal area: Melaxineinae, shell with median umbones, round (Cretaceous-Recent: *Melaxinea*). Vasconellinae Scarlato & Starobogatov 1979, shell irregularly tetragonal, umbones shifted forward (Eocene: *Vasconella*).

Praecardioidea. Ligament alvicular amphydethic, true dentition absent. Praecardiidae Hoernes 1884 (Silurian-Devonian: *Praecardium, Buchiola*). Necklaniidae Scarlato & Starobogatov 1979, shells oval, equilateral with opthogyrate umbones and fine radial sculpture (Silurian: *Necklania, Slava*). Cardiolidae Fischer 1886 (Silurian-Carboniferous: *Cardiola, Opisthocoelus*).

Noetiodea. Ligament alivincular, often with a tendency to prosodety, with equal transversal thickenings, umbones often opisthogyrate, shifted forward, seldom backward. Trinacriidae McNeil 1937: Striarcinae McNeil 1938 (Cretaceous-Recent: *Striarca, Galactella, Arcopsis, Ovalarca, Trigonodesma, Vetoarca*). Trinacriinae McNeil 1937 (Cretaceous-Eocene: *Trinacria, Linter, Pachecoa*). Noetiidae Steward 1930 (Cretaceous-Recent: *Noetia, Noetiopsis, Arginopsis, Protonoetia, Sheldonella*). Litharcidae Scarlato & Starobogatov 1979, teeth short, nearly vertical in a continuous row, ligament prosodethic, umbones shifted backwards (Recent: *Litharca*).

Gryphaeoidea. Gryphaeidae Vialov 1936 (Triassic-Recent): Gryphaeinae (Triassic-Jurassic: *Gryphaea, Catinula, Deltoideum, Liostrea, Pernostrea, Praexogyra*). Pycnodonteinae Stenzel 1959 (Cretaceous-Recent: *Pycnodonte, Neopycnodonte, Texigryphaea*). Hiotissinae Scarlato & Starobogatov 1979, shell with distinct radial folds (Cretaceous-Recent: *Hyotissa*). Exogyridae Vialov 1936: Exogyrinae (Jurassic-Cretaceous: *Exogyra, Aetostrea, Amphidonte, Ceratostreon, Hymatogyra, Nanogyra, Planospirites, Rhynchostreon, Vultogryphaea*). Gryphaeostreinae Stenzel 1971 (Cretaceous-Miocene: *Gryphaeostrea, Gyrostrea*).

Ostreoidea. Crassostreidae Scarlato & Starobogatov 1979, promyal passage present: oviparous (nonincubatory) forms (Cretaceous-Recent: *Crassostrea, Acutostrea, Pseudoperna, Saccostrea, Striostrea*). Ostreidae Rafinesque 1815: Lophinae Vialov 1936 (Triassic-Recent: *Lopha, Alectryonella, Camelolopha, Nicaisolopha, Rastellum*), Ostreinae (Cretaceous-Recent: *Ostrea, Cubitostrea, Ferganea, Platygena, Sokolowia*), Flemingostreinae Stenzel 1971 (Cretaceous-Miocene: *Flemingostrea, Kokanostrea, Odontogryphaea, Ostreonella*).

Limopsoidea. Pichleriidae Scarlato & Starobogatov 1979, anterior field of the valve distinctly separated, cardinal area straightened, of regular width (Triassic: *Pichleria, Hofferia*). Limopsidae Dall 1895 (Jurassic-Recent: *Limopsis, Emplectonia, Nipponilimopsis, Lissarca*).

Phylobryoidea. Auporiidae Scarlato & Starobogatov 1979, anterior teeth present (Pliocene-Recent: *Auporia*). Phylobryidae Bernard 1897 (Eocene-Recent: *Phylobrya*).

Ptychodesmatoidea. Ligament duplivincular with a very short anterior part, nacreous layer developed. Ptychodesmatidae Scarlato & Starobogatov fam. nov., umbones occupy anterior position, dentition of cyrtodont type (Ordovician-Devonian: *Ptychodesma*).

Arcoidea. Ligament duplivincular equilateral with chevrons on the ligamental area: structure of dentition does not change with shift of ligament. Nordenskjoeldiidae Scarlato & Starobogatov 1979, anterior teeth diverge fanwisely, posterior ones horizontal (Carboniferous-Cretaceous: *Cucullopsis, Nordenskjoeldia*). Parallelodontidae Dall 1898 (Ordovician?-Devonian-Jurassic: *Parallelodon*). Grammatodontidae Branson 1942, teeth horizontal posteriorly, oblique anteriorly, with smooth transition in the middle of the row (Jurassic-Cretaceous: *Grammatodon*). Barbatiidae Scarlato & Starobogatov 1979, teeth oblique, arranged in two groups, separated or contiguous; shell elongated, fine-ribbed: Calloarcinae Scarlato & Starobogatov 1979, anterior and posterior teeth strongly oblique, join in the middle nearly vertically (Cretaceous-Recent: *Calloarca, Cucullacarca*), Scaphulinae Scarlato & Starobogatov 1979, teeth oblique (especially posterior ones), groups of teeth separated in the middle (Jurassic-Recent: *Eonavicula, Scaphula, Trisidos*). Barbatiinae, teeth slightly oblique, both rows long, contiguous (but separated) in the middle (Triassic-Recent: *Barbatia, Arca, Fulgeria*). Anadaridae Reinhart 1935, teeth vertical, two rows noticeably separated in the middle, shell massive, with thick ribs: Anadarinae, umbones nearly orthogyrate, rows of teeth almost do not narrow to the middle (Cretaceous-Recent: *Anadara, Larkinia, Scapharca*), Seniliinae Scarlato & Starobogatov 1979, umbones sharply prosogyrate, rows of teeth narrow to the middle (Recent: *Senilia*). Arcidae Rafinesque 1815, row of teeth continuous (Cretaceous-Recent: *Arca*).

Glycymeridoidea. Ligament duplivincular equilateral with chevrons on the ligamental area; ligamental shift changes the structure of dentition with growth. Idonearcidae Scarlato & Starobogatov 1979, anterior and posterior teeth horizontal, middle ones vertical, between them teeth bent as an angle (Jurassic-Cretaceous: *Idonearca*). Lopatiniidae Scarlato & Starobogatov 1979, shell roundish, median teeth diverge fanwisely from the umbone, anterior and posterior ones parallel to the edge (Cretaceous: *Lopatinia*). Glycimeridae Newton 1922: Arcullaeinae Newell 1969 (Cretaceous: *Arcullaea, Peruarca, Pettersia, Protoarca, Trigonoarca*), Glycimeridinae (Cretaceous-Recent: *Glycimeris, Axinactis*).

Some genera from Paleozoic and Mesozoic deposits which were referred to the superfamily Mytiloidea should be excluded from this superfamily and included into Ambonychioidea and Modiomorphoidea.

The diversity of ligaments in arcoids and structure of the shell of *Ptychodesma* (Carter & Tevesz, 1978) erase distinctions between the suborders Mytileina and Cyrtodontina. These two suborders should be united. Then, two more superfamilies will be added to the lowest Mytileina.

Cyrtodontoidea. Cyrtodontidae Ulrich 1894 (Ordovician-Devonian: *Cyrtodonta, Cyrtodontula, Ortonella, Pharcidoconcha, Thorslundia, Vanuxemia, Warburgia*). Matheriidae Scarlato & Starobogatov 1979, umbones near the anterior end of the shell, posterior teeth missing (Ordovician-Silurian: *Matheria, Heivea, Sowteria*).

Limarcoidea. Limarcidae Scarlato & Starobogatov 1979, valves elongated dorsoventrally, two to three subumbonal teeth present, posterior teeth long, sometimes striated (Paleocene-Recent: *Limarca, Cratis*).

This revision of the systematics of the suborder Mytileina was not included in the earlier prepared work of Scarlato & Starobogatov (1979). This revision is an addition to the earlier work.

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LIFE FORMS AND ECOGENESIS OF THE CEPHALOPODS IN THE PALEOZOIC

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Abstract

The five main adaptive types (life forms) characterizing the ecological structure of Recent taxocoens of cephalopods

can be distinguished among fossils, too. The constructive peculiarities of the shell, which reflect hydrostatic or hydrodynamic properties of the animal and permit or forbid the development of definite adaptive potentials, can serve as criteria of differences in cephalopods. The degree of flotation is determined by relative proportions of phragmocone and living chamber and is a function of the apical angle (in ortho- and cyrtoconic shells) and of spiral increasing rate (in coiled forms); the degree of activity of floration is reflected in the proportions of the soft body, shape of aperture and the degree of development of hyponomic sinus. Additional criteria, the structure of siphon, development of chamber and intrasiphonal deposits, the character of sculpture, serve for evaluation of possibilities and ways of maintenance of equilibrium position in water, fairness, etc. The structure of initial parts of the shell, the frequency of occurrence in deposits suggest a demersal or pelagic mode of reproduction, a swarming or solitary mode of life.

Benthic life forms include ortho- and cyrtocones possessing minimum flotation, open wide aperture (*Multicameroceras, Burenoceras* - Ellesmerocerida; *Rizosceras, Macrodomoceras* - Oncocerida; *Platyconus* - Discosorida; *Dentoceras* - Nautilida; *Manchuroceras* - Endocerida; Gonioceratidae - Actinocerida) and forms with a tower-shaped spirally conical shell (*Forsteoceras, Mitroceras* - Oncocerida).

Bathypelagic life forms are characterized by wide conical ortho- and cyrtocones with a narrow slanting aperture or annulated shell characters of hypostome adaptation (*Bridgeoceras, Plectronoceras* - Ellesmerocerida; *Boreoceras* - Endocerida; Parapharagmitidea - Orthocerida; *Phragmoceras* - Discosorida; *Oncoceras* - Oncocerida), forms with quickly broadening involute coiled shells resembling constructively *Nautilus* and gyroconic heteromorphs like *Angelinoceras, Joiletoceras* (Tarphicerida).

Nectobenthic life forms include narrow conical ortho- and cyrtocones with rather high flotation and with well-developed mechanisms for orientation and stabilisation of a shell in a position suitable for active swimming; among coiled forms there are moderately evolute ones with a moderate broadening rate and proportions of living chamber permitting a development of functionally active mantle cavity.

Necton life forms are mainly streamlined ortrocones with developed mechanisms for horizontal orientation (*Bactroceras* - Ellesmerocerida; *Suecoceras* - Endocerida; *Plagiostomoceras, Hemicosmorthoceras* - Orthocerida; *Aktjubocheilida* - Oncocerida; *Uchtoceras* - Discosorida) and among coiled forms like *Artinskia* (Agoniatitida), *Eumorphoceras* (Goniatitida), *Paradomatoceras* (Nautilida).

Transition to a planctonic way of life is expressed in acquirement of adaptations to constant hypostome position and soaring in water (closed aperture, annulated shell, spines, appendages, collars), to pelagic life at early stages (small size of initial parts of the shell, spherical protoconch). Poor mobility is reflected in non-typical proportions of soft body which do not permit the development of a functionally active mantle cavity. Ortho- and cyrtocones – *Catoraphiceras* (Ellesmerocerida), annulated Orthocerida and Pseudoorthocerida, *Endocycloceras* (Endocerida), Hemiphragmoceratidae (Oncocerida), Phragmoceratidae (Discosorida). Coiled forms: slowly broadening evolute with vermicular soft body and "semicoiled" (*Ophioceras*, Estoniocerátidae - Tarphicerida; *Erbenoceras* - Agoniatitida; Gastrioceratacea - Goniatitida; *Holconautilus* - Nautilida); slowly broadening involute – subspherical thick discoidal (*Prolobites* - Agoniatitida; *Protopopanoceras* - Goniatitida; *Epiwocklumeria* - Clymeniida), thin discoidal (*Uchtites* - Agoniatitida; *Terektites* - Goniatitida).

Analysis of more than 900 genera and 14 orders of Paleozoic cephalopods has enabled us to establish specificity of adaptive specialization of each order and, by changes in the relation of life forms during the evolution of individual orders and class as a whole, to distinguish three stages of ecogenesis. 1) From the origin of cephalopods to the Middle Ordovician – a stage of acquirement of adaptations to demersal pelagic life; most genera belonged to benthopelagic life forms. 2) From Middle Ordovician to Devonian – a stage of active conquering pelagial; a relative number of pelagic forms reached 50% of all existing genera by the beginning of the Devonian. 3) Devonian-Permian – a stage of stable relationships between all life forms; ecological structure of the fauna of cephalopods at this stage did not nearly differ from the recent one, though taxonomically had nothing in common with it.

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TAXONOMY, PHYLOGENY AND ECOLOGICAL RADIATION OF SQUIDS OF THE FAMILY OMMASTREPHIDAE

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Abstract

The progressive evolution of squids (the suborder Oegopsida) proceeded in the direction of nectonisation. Members of the family Ommastrephidae are at the top of this process. A scheme of their phylogenetic relations was constructed. Three main stages and an intermediate one (Ornithotenthinae) are distinguished in the evolution of the family. Members of *Illex* are closest to the initial type morphologically and species of *Todaropsis* are closest ecologically.

Ecological expansion of the family proceeded from the coast into oceanic pelagial. The initial biotope is a zone of transition from the shelf to the continental slope (*Illex, Todaropsis, Martialia, Nototodarus nipponicus* Okutani & Uemura). The occupation of waters of the open ocean by ommastrephids occurred simultaneously with acanthopterygians, in early Oligocene-Miocene presumably. During the occupation of oceanic pelagial in phylogenesis of the family correlated changes in morphology, ecology and behavior took place: the appearance of luminescent organs, pelagisation of egg laying, change of types of communities, increase in activity, mobility, and reactions to the environmental stimuli and, as a result, improvement of the organization of active nectonic organism.

At every main stage in the evolution of ommastrephids, there is a group approaching the optimal organization of the nectonic organism; directions of its improvement can be outlined: *Illex* - *Todarodes, Nototodarus sloani* (Gray)

-*Ommastrephes, Sthenotenthis - Dosidicus*. In the above forms, a group progress is accompanied by biological progress and they are characterized by a strict allopatricity of areas. At all stages of the family evolution, a number of deviations was observed in the direction of telogenesis. In primitive forms (*Todaropsis, Martialia, Nototodarus nipponicus*), this is displayed in changes of the proportions of the body optimal for nectonic organism, while, in more advanced forms (*Ornithotenthis, Eucleotenthis, Hyalotenthis*), in the decrease of size.

There is a discrepancy between a large distribution area of the family with great variety of climatic and biotic conditions and extremely low level of taxonomic radiation. The main cause of this is that the family as a whole is at the top of the main direction of group progress of squids and is one of the leading groups in the coevolution of Cephalopoda and fishes (Nesis, 1975).

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SOME PECULIARITIES OF LARVAL DEVELOPMENT OF SQUIDS OF THE FAMILY ENOPLOTEUTHIDAE FROM THE CENTRAL-EAST ATLANTIC

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Abstract

The purpose of this work is to elucidate the early ontogenetic stages of squids of the family Enoploteuthidae and peculiarities of larval development of its most abundant species. Samples were taken by the net IKS-80 from the standard horizons of 0.50 and 100 m in all seasons. Two thousand six hundred samples were examined; larvae were found in 24% of the samples.

The squids were identified by the series method, i.e., larval specimens from the largest to smallest ones were selected. The main measurements were done on Okutani & McGowan (1969). The larvae of four species (*Abraliopsis morisii* (Verany), *Abralia veranyi* (Rüppell), *Ancistrocheirus alessandrinii* (Verany) and *Pterygioteuthis giardi* Fischer) were identified.

In most abundant species, the successive developmental stages were established on the basis of the appearance of photophores on the ventral arms (*Abraliopsis morisii*) or intramantle photophores (*Pterygioteuthis giardi*) that defines roughly the morphological changes occurring during the transition of larva to postlarva.

Four stages were established for *Abraliopsis morisii*: 1) stage without photophores (mantle length 1.5-3.1 mm); 2) stage with one photophore on the ends of the ventral arms (mantle length 2.7-3.8 mm); 3) stage with two photophores on the ventral arms; photophores appear on eyes, at the base of the fourth pair of arms and on the ventral surface of the mantle (mantle length 3.7-5.5 mm); 4) stage with three photophores on the arms of the fourth pair; numerous photophores appear on the ventral surface of mantle, head and eyes (over 5.5 mm). Virtually it is a small squid with its all morphological characters.

Four stages were established also for *Pterygioteuthis giardi*: 1) stage without photophores (mantle length is less than 1.9 mm); 2) stage with one pair of anal photophores; one photophore on each eye (mantle length 1.9-2.5 mm); 3) stage of branchial photophores; three photophores on each eye (mantle length 2.9-4.0 mm); 4) stage of ventral photophores (mantle length more than 4.5 mm). Eight intramantle photophores, paired anal and branchial and four unpaired ventral. Nine to 10 photophores on eyes.

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THE LIMITS OF STEPWISE ADAPTATION OF *MACOMA BALTICA, MYTILUS EDULIS* AND *MYA ARENARIA* TO DIFFERENT SALINITIES IN THE EASTERN PART OF THE BALTIC SEA

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Abstract

The bivalve mollusks *Macoma baltica* (Linnaeus), *Mya arenaria* Linnaeus and *Mytilus edulis* Linnaeus stand a rather wide range of salinity in various parts of their distribution area. In the Baltic Sea, these species occur at the low salinity limit of the true marine fauna existence. Works by Belyaev (1957) and Karpevich & Shurin (1968) have shown an ecological spectrum of salinity adaptations of these species. However, we consider experiments at a modern physiological level quite necessary.

A considerable role in adaptations of marine mollusks to deviations in salinity belongs to the cells' resistance (Schlieper, 1958; Zhirmunsky, 1962; Yaroslavtzeva & Zhirmunsky, 1978) and to the behavioristic reaction of the organism – closing the valves (Belyaev, 1957). Closing the valves as a response of mollusks to decreased salinity of water is a test for a determination of species activity in different salinities.

The bivalve mollusks *Macoma baltica, Mytilus edulis* and *Mya arenaria* were investigated. The work was conducted at the White Sea Biological Station of the Zoological Institute, Academy of Sciences of the U.S.S.R., on the material collected in August 1977 in Maatsalu, Hapsalu and Virteu bays of the Baltic Sea. After a fortnight acclimation of mollusks to 7°/oo (initial salinity), they were placed into different salinities for a determination of their tolerance.

It has been established that a salinity of 4-30°/oo is an optimal zone for *Macoma*. In this zone, the mollusk displays 100% activity. In a zone with low transitional concentrations of water, the activity changed from 50% to 60%

at 1°/oo and 3°/oo, respectively. Fresh water should be considered an extremely low border, though in fresh water certain activity was observed, too: after four days maintenance in fresh water, 10% of the mollusks were active; after five days, 50%; and on the following days the mollusks quickly died.

Mya arenaria was found to be a more euryhaline species. For this mollusk, the optimal salinity limits were from 1-30°/oo. Fresh water and salinity higher than 30°/oo are unfavorable. The activity of *Mya* was determined by the number of filtrating individuals. The mollusk ceases the filtration earlier than it draws the siphon into the shell. This, apparently, is due to the presence of two types of receptors. Chemoreceptors give a signal to cease the filtration, and osmoreceptors give a signal to draw in the siphon.

The most narrow range of salinity was recorded for *Mytilus edulis*. The salinity limits of its normal vital activity were from 5-25°/oo.

The determination of the species' resistance at the organismal level has shown that species with tightly closing shells can for a long time withstand unfavorable salinities (nine to 20 days in *Macoma* and to two weeks in *Mytilus edulis*. One hundred percent mortality of *Mya* in fresh water took place in nine days; in water of 35 and 40°/oo all specimens died in two days.

A study of the osmotic concentration of mantle fluid has shown that isotony of the external and internal medium typical of poikilosmotic organisms is observed in all species only at the salinity close to the initial one. With its fall, the osmotic pressure of the mantle fluid exceeded to a certain extent that of the external medium.

Experiments have shown that some Baltic mollusks possess rather high physiological plasticity and can withstand desalting. However, in highly desalted (less than 4°/oo) parts of the Baltic Sea, these species do not occur. Apparently, it is due to the fact that the resistance of marine animals to desalting can vary considerable in ontogenesis, and earlier stages of the individual development are less tolerant to changes in salinity.

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THE MARINE PALEOGENE GASTROPODS FROM THE SOUTH OF THE U.S.S.R.

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Abstract

For paleoecological stratigraphic and other conclusions, it is important not only to study individual faunistic complexes but to compare them and explain the causes of their differences. These differences can be secondary in their character, if forms occurred in a basin but their shells for some reasons have not preserved, or primary ones associated with a real lack of forms in a basin. The primary differences can be divided into chromological ones (associated with the appearance and extinction of taxa), geographic (isolation of basins), biogeographic (temperature zonality) and ecological (local abiotic and biotic factors).

In marine Paleogene deposits from the South of the U.S.S.R., the remains of gastropods are distributed extremely unevenly. Most rich and best preserved they are in the Ukraine: Luzanovka of the Cherkassy district (Lower Paleocene), Kostianets near Kanev (Middle Eocene) and Mandrikovka, a part of the city of Dnepropetrovsk (Upper Eocene). Regardless of their different geological age, complexes have some common features due to the identical type of fossilization and persistence and to similar ecological conditions in basins (shallow subtropical sea of normal salinity with sandy bottom). In Luzanovka and other Paleocene complexes, unlike in younger ones, there are representative of ancient extinct groups (Procerithiidae, Euomphalidae?) and no members of Sinidae, Conidae or Terebridae, which did not, apparently, exist in the Paleocene. But, in general, at the beginning of the Cenozoic the composition of the families was close to a recent one; in Luzanovka exist most of the families known in the Paleogene in the south of the U.S.S.R. Chronological differences between the faunas of Luzanovka and Mandrikovka are displayed partly in the generic but mainly in the specific composition: there is no one common species of gastropods in these complexes.

In Transcaspian, the Cheganian beds, which are of the same age of Mandrikovka ones, contain the best complex of gastropods. The Cheganian complex resembles the Mandrikovka one in having many common species, but is considerably poorer. Unlike the Ukrainian complexes, the Cheganian fauna occurs over a vast area, but everywhere shells are frayed and almost no protoconchs nor young specimens have been found. It is possible that forms with small shells (Rissoacea, Lamnidae, etc.) lived in the basin but have not remained preserved up to now; other groups are missing due to ecological reasons. In Cheganian, there are no forms with cap-like shells (excluding Calyptraeidae) because of the lack of suitable grounds; members of Trochacea and Cerithiacea are very rare, because these groups are relatively euryhalinous and flourish in coastal areas with inflow of fresh water, where they easily withstand competition with more polyhalinous organisms; in the Cheganian Sea, the salinity was high everywhere.

Younger (Oligocene) complexes are very similar throughout a vast territory (the Crimea, Ukraine, North Caucasus, Transcaspian), but much poorer as compared to Paleocene and Eocene ones. Turritellidae, Xenophoridae, Rostellariidae, Conidae and some genera of other families typical of the Eocene vanish or become very rare. In general, these are warm-water groups; subtropical basins turned into temperately warm-water ones. Aporrhaidae, Cassididae, Muricidae, Turridae and some genera of Fasciolariidae have become dominant; these groups happened to be more eurythermal, though some of them occur now in tropical and subtropical seas.

Complexes of Armenia and Nakhichevan A.S.S.R. differ from the above complexes. The composition of Late Eocene gastropods from these regions is poorer than that of the Ukraine and even Transcaspian. Well represented are Trochacea, Cerithiacea, Cypraeidae, Terebellidae, large Globulariidae, Conidae; the similar composition remained in the Oligocene (Shargaburian beds of Armenia); in addition to mollusks, reef-forming corals are very abundant. These complexes are tropical. Apparently, the cooling in the north regions at the boundary of the Eocene and Oligocene did not spread to the basin of Armenia.

At the time in question, the sea of Armenia and of adjacent regions belonged to the Mediterranean biogeographic area and other seas of the south of the U.S.S.R. to the North-European area. The faunas of Georgia and most parts of Azerbaijan are of intermediate character, but nevertheless gravitate towards a northern type. In addition to temperature zonality, the faunistic differences are associated, apparently, with some geographic barriers which separated the basins.

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ON THE HOMEOMORPHY OF BIVALVIA IN THE NEOGENE BASINS OF THE EAST PARATETHYS

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Abstract

The Neogene of the East Paratethys is characterized by the development of successive semiclosed and closed basins with low salinity and a peculiar living world. Among endemic and specific bivalve molluscs here often appeared homeomorphs resembling the forms from the preceding basins but having no direct relationship with them.

In semimarine semiclosed basins (e.g., Tschokrakian and late-Konkian basins) with decreased salinity, certain impoverishment of the fauna took place. But those few new endemic species which appeared here differed but little in their habitus (e.g., *Acanthocardia impar* (Zhizhchenko) from Tschokrakian and *A. andrussovi* (Sokolov) from Konkian (Merklin, 1966), *Cerastoderma bogatchevi* (Kolesnikov) from Tschokrakian and *C. praeplicatum* (Hilber) from Konkian (Bagdasarian, 1974)).

In semimarine closed waterbodies (Sarmatian and Akchagylian) with a considerably lower salinity, only a few representatives of euryhaline genera remained. In progressive eurybionts (Merklin, 1966), intraspecific variability increased and, as a result of outbreaks of speciation, a great number of new species and even new genera appeared. Many new species appeared, especially in the families Cardiidae and Mactridae. Often they differed from initial forms in habitus, but sometimes were very similar between each other though separated by about 7 million years. On the basis of their external similarity, some authors (Ali-Zade, 1967) believe that the Akchagylian fauna (up to 25 species of Cardiidae and 10 species of Mactridae) originates directly from the Sarmatian one, which might have survived in some asylums. Most investigators connect this phenomen with homeomorphic evolution. Studies of Cardiidae species conducted by us (Paramonova, 1977) also have shown that morphological differences between Akchagylian "descendants" and Sarmatian "ancestors" run counter to the conclusions on their direct affinity. The lack of genetic relations between them is proved also by microstructural studies (Popov, 1974). Akchagylian *Avimactra* resembles sometimes by its shape Sarmatian *Mactra* but differs considerably from the latter in the structure of hinge and the position of submerged numph at the border with chondrophore.

In brackish-water closed basins (Pontian, Kymmerian and others), ion composition apparently changed, too, due to a great decrease in salinity. Most important here were brackish-water Cardiidae with greater intraspecific variability and higher speciation rate. A great number of new genera appeared among them, representatives of which in a number of cases fully or partly resembled some species of Sarmatian *Cerastoderma*.

A wide development of homeomorphy in the Neogene semiclosed and closed basins of the East Paratethys is stipulated, as was indicated many times by genetic similarity of ancestral species repeatedly immigrating here from the Mediterranean area and by their further development under similar conditions.

Davidashvili (1970) considers the evolution of the Sarmatian and Akchagylian faunas as a bright example of parallelism in the phylogenetic development, which, according to Darwin, proceeds on the basis of analogous variability or, according to N.I. Vavilov, on the basis of homologous variability. Since homeomorphs did not appear here in simultaneously existing series but in successive ones, iteration would be a more accurate notion than parallelism in this case. Undoubtedly, some homeomorphs could arise in these basins owing to homologous variability. In closely related forms, homology of genes results in the appearance of homologous mutations (Vorontsov, 1966). In similar niches under the similar effect of selection, they produce homologous forms. Homeomorphs arise, apparently, as a result of foetalization, which widely spread among bivalve molluscs.

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ANTHROPOGENE MARINE FAUNA OF MOLLUSCS OF KAMCHATKA, CHUKOTKA AND ALASKA AND SOME PROBLEMS OF THE MALACOFAUNAL HISTORY OF THE BERING SEA

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Abstract

Until now, the history of formation of malacofauna from temperate waters of the northern Pacific has been poorly known, due to our scanty knowledge of young water masses in this region. Geological, paleontological and paleomagnetic data obtained during recent years have enlarged considerably information on the contents and distribution of the fauna of gastropods and bivalves from the Bering Sea and neighboring marine basins at some stages of the Neogene and Antropogene (the last 2 million years).

At present, in the Antropogene deposits of eastern Kamchatka (Kamchatka Peninsula and Karaginsky Island),

four complexes of molluscs differing in the number of extinct forms and biogeographic composition can be distinguished. These complexes of molluscs correspond to different periods of time of geological history (from more than 1 million years to less than 0.1 million years) and are divided by interruptions in sediment accumulation.

The Olkhovkian complex of the end of the Pliocene, Eopleistocene and the beginning of the Early Pleistocene is close to the Recent malacofauna of the Beringian high boreal subregion (Komandor, Anadyr and East-Chukotka provinces). This complex is characterized by the presence of such Arctic species as *Astarte (Nicania) montagui fabula* (Reeve), *A. (N.) montagui warhami* (Hancock) and *Nuculana lamellosa lamellosa* (Leche).

The Karaginian complex of molluscs of the end of the Early Pleistocene shows a definite similarity with Recent faunas of the Anadyr and East Chukotka provinces. It is characterized by a mass distribution of the Arctic species *Nuculana lamellosa lamellosa* and *Portlandia arctica* (Gray).

The Ossorian complex of the second half of the Middle Pleistocene is the most cold water complex in the whole Antropogene. Apparently, a fauna of molluscs close to the Recent fauna of arctic seas was developed throughout the Bering Sea at that time. Typical for the Ossorian complex are *Portlandia arctica, Yoldiella intermedia* (M. Sars), *Y. lenticula* (Möller), *Astarte (Tridonta) borealis placenta* (Mörch) and *A. (N.) montagui striata* (Leach).

The Attarman complex of molluscs of the beginning of the Late Pleistocene is, on the contrary, the most warm water Antropogene complex. It is characterized by the absence of arctic forms, sharp predominance of widely distributed boreal species and the presence of low boreal *Protothaca adamsi* (Reeve) and *Macoma orbiculata* Scarlato living now in more southern regions.

The formation of malacofauna of the Bering Sea in the Antropogene was carried out, in general, on account of the formation of local boreal arctic forms and the migration of most cold-loving elements from the Arctic, with a simultaneous increasing cooling of the climate.

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ECOGENESIS OF BIVALVE MOLLUSCS IN THE BALAKHONIAN SERIES FROM THE KUZNETSK BASIN

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Abstract

Bivalve molluscs in the Balakhonian series from the Kuznetsk Basin give us a possibility to trace the history of the development of paleoecological conditions from the early Carboniferous to the Permian. During the formation of the Balakhonian series, one can observe a gradual transition of the marine regime to estuary, lagoon, lake and, at last, river regime.

The Ostrogian beds are characterized by a rather poor fauna of desalted estuary water bodies which appeared ater the sea regression. For a short period of time, estuaries transformed into sea gulfs and shallow seas of normal salinity. At the end of the Ostrogian period were formed conditions of a brackish lagoon which had limited communications with an open sea.

The fauna of the Mazurovian beds is poorly studied. It, apparently, was characteristic of lake basins connected with estuaries.

More diverse and very abundant fauna of the Alykaevian beds points to often changed paleoecological conditions. Widely distributed were changeable estuary basins which, at the beginning, were salted enough, nearly as lagoons, and then gradually became desalted.

Sometimes large freshwater basins appeared which had from time to time connections with estuaries and through them limited communications with the sea.

Intermediate beds are characterized by quite different paleoecological conditions. Bivalve molluscs inhabited shallow closed lagoons with low salinity. Such water bodies were formed in the place of estuaries of gradually regressed sea. In the Ishanovian age, very poor but peculair fauna of bivalves testifies to a considerable increasing in salinity of some lagoons. After this, an abrupt change of the fauna takes place in the Kemerovian beds and freshwater forms gain dominance. In the Usiatian age, the age of intensive coal formation, shells of freshwater bivalves gained maximum sizes. They were widely distributed and inhabited large lakes of river impoundment areas.

Ecogenesis of bivalves of the Kuznetsk basin from the Carboniferous to the Permian proceeded in the direction from marine to freshwater conditions. Bivalves responded very sensitively even to very negligible changes in the environment. Within the beds, paleosuccession changes of tanatocoenoses were predominant. Differences between faunistic complexes of each bed depended not only on paleoecological causes but also on evolutionary changes of species. A frequent change of faunistic complexes of the Balakhonian series was associated, in general, with repeated freshening of basins of seas of the Carboniferous period. Under such conditions, marine and brackish-water species were doomed to extinction, since, due to their physiological characters, they could not adapt to the life in freshwater basins. During transgressions, freshwater forms easily adapted to marine conditions. A mass appearance occurred not only of individuals belonging to one species but also of many species and even genera, due to a mixture of marine and freshwater elements.

All said above shows that a study of ecogenesis of bivalves of the Balakhonian series of the Kuznetzk Basin is of both theoretical and great practical importance for ecostratigraphy of Carboniferous deposits of the Late Paleozoic of Siberia. Paleoecological succession of bivalves enables us to distinguish marking horizons in the limits of very small stratigraphic intervals that is of great importance for conducting geological prospecting work.

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RESULTS OF A STUDY OF PROSOBRANCH MOLLUSKS AND FAUNA OF THE NON-GROUND BENTHIC SUBSTRATA

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Abstract

Of the 20 most primitive families of Recent Gastropoda belonging to the subclasses Cyclobranchia and partly to Pectinibranchia, members of 10 families inhabit non-ground substrata, which are sometimes alien to bental. Such forms were not found among the Scutibranchia.

Some representatives of the Nacellidae, Patellidae and Acmaeidae inhabiting, as a rule, rocky grounds have adapted to a life of living on bottom plants, such as macrophytic algae and sea grass. Among the Acmaeidae, in the genus *Collisella* there are species living on the shells of other Gastropoda; *Potamacmea fluviatilis* (Blanford) was found on tree trunks and corpses in estuarine parts of rivers in India. Some species of Lepetidae and Pectinodontidae occur on pieces of submerged wood. All representatives of Bathysciadiidae and Bathypeltidae inhabit the beaks of cephalopods and probably utilize them.

Of the Lepetellidae, *Lepetella tubicola* Verrill settles on chitinous tubes of the polychaete *Hyalnaecia artifex* Verrill. Of the Bathyphytophilidae, *Bathyphytophilus caribaens* Moskalev occurs on leaf plates and on roots of *Thalassia testudinum* König, getting from the upper subtidal zone into the ultraabyssal (hadal). Of eight described genera of Cocculinidae, their members occur on submerged wood and *Teuthirostria cancellata* Moskalev on beaks of squids.

For the main type of taxonomic investigations were chosen world revisions of taxa not lower than family groups with standard requirements for similar taxa of different groups. When studying systems of taxa of a relatively high rank, only such an approach gives a possibility of determining the taxonomic distinction of the abyssal fauna and the rank or endemism in defining the zoogeographic rank of a region.

Analysis of feeding and substrata inhabited by some studied mollusks shows that these factors are the main ones in the vertical distribution of these organisms. They can be arranged into five trophic groups: xylophags, fungophags, herbaphags, chitinophags and phytophags-euryphags. Each of these groups of mollusks possesses a specific type of structure of radula as an organ of food destruction.

In a number of cases, it is possible to consider the eurybathic distribution of an organism as a result of wide food specialization and abyssal endemism as a result of food specialization.

It should be accepted that there is no direct connection between the age of the group and depth of its penetration into the ocean. Thermophilous groups, which have a narrow range of food objects, could not reach great depths. Paleotemperature conditions of the origin of groups, their trophic plasticity, universal mouth parts and wide vertical distribution of food objects are apparently all factors which provided a success in conquering depths.

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THE ABYSSAL AND THE UPPER ULTRAABYSSAL BUCCINIDAE (*SENSU LATO*) OF THE OCEAN

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Abstract

Buccinidae *sensu lato* belonging to subtidal-bathyal and bathyal-upper ultraabyssal (upper hadal) genera from the northern hemisphere do not overcome depths of 4000-4500 m and do not spread southward of 40° N.L. The lower border of their distribution coincides with the depth where calcium dissolving begins. These genera occur only on continental and insular slopes of abyssal trenches of the northern hemisphere.

At a depth of 4000-4500 m, new abyssal genera of Buccinidae appear: *Tacita*, widely distributed in the Pacific up to the Peru-Chile trench; *Calliloncha*, a monotypical genus from the Idzu-Bonin trench.

A similar phenomenon takes place, apparently, in subpolar waters of the southern hemisphere, e.g., in the Atlantic and Indian sectors of the South Ocean. Members of the Buccinidae are now known from the southern Atlantic from a depth of over 7000 m. This previously unknown species and genus is from the South Sandwich abyssal trench. Up to this finding, buccinids from this region were known only from depths of no more than 4000 m. Genera from the northern and southern hemispheres belong to different families.

Distribution of buccinids within the abyssal and upper ultraabyssal (hadal) of the Ocean occurs from the north and from the south; in the distribution, participate members of the genera connected genetically with subpolar waters.

Some anatomic characters (e.g., structure of the digestive system – the presence of large gland of Leiblein and pharynx of Leiblein, stomach in the shape of a thin-walled sac with closely located and shifted forward oesophageal and small intestine openings) suggest that only evolutionary advanced representatives of buccinids penetrate the abyssal and upper hadal depths.

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THE SPECIES COMPOSITION AND PECULIARITIES OF THE ECOLOGY OF THE SACCOGLOSSA IN THE BARENTS SEA AND WHITE SEA

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Abstract

In June-September of 1972 to 1977, intertidal collections of Saccoglossa in the Barents and White seas were conducted. Four species of Saccoglossa were found: *Limapontia capitata* (Müller) (Dalnie Zelentsy), *L. depressa* Adler & Hancock (Dalnie Zelentsy), *L. cocksi* (Adler & Hancock) (Great Ainov Island, Kharlov Island, Dalnie Zelentsy, Cape Kanin Nos, Sosnovets Island, Solovetskie Islands, Rugozero Inlet, White Sea) and *Alderia modesta* (Loven) (Dalnie Zelentsy). *L. depressa* was recorded from the Soviet waters for the first time.

In the Barents Sea, all four species of Saccoglossa occur. According to their ecology, they can be arranged into two groups: 1) inhabitants of the lower supratidal and upper intertidal of salty marshes reaching high density in the places of aggregation of *Vaucheria*, which serves as a substratum and food for molluscs (*Limapontia depressa, Alderia modesta*); 2) inhabitants of shallow upper intertidal pits in the rocks with abundant *Acrosiphonia* and *Cladophora*, which serve as food for molluscs (*L. capitata, L. cocksi*). From the White Sea, only *L. cocksi* was recorded. It was found in great abundance in the Rugozero Inlet (September 1976) on filamentous algae in pools, on gently sloping sandy banks beginning from the lower supratidal among thickets of *Salicornia europea* Linnaeus and *Aster tripolium* Linnaeus to the zone of *Aacophyllum nodosum* Le Jolis. Large layers of drying filamentous algae, where the remains of water are preserved, provide for *L. cocksi* sufficient humidity to withstand the drying period.

Contrasting in their coloration (in relation to the background – green filamentous algae), always brightly black *Limapontia capitata* and *L. cocksi* almost do not differ from the young of periwinkles, edible mussels and other molluscs of black color covering in summer thalluses of *Acrosiphonia* and *Cladophora*. The coloration of *L. depressa*, and especially that of *Alderia modesta*, varies to a high extent. However, each color variety has its own suitable background of greenish, black, grey, brownish and yellow spots, which make the coloration of the upper layer of the ground of marshes. During the low tide, *L. capitata* and *L. cocksi* take shelter in a mass of damp filamentous algae. *Alderia modesta* and *L. depressa* submerge almost completely into the loose ground, which always contains some water, thus protecting themselves from the destructive effect of drying. In this case, *A. modesta* often turns on the back and lowers its papillae into remains of water.

The four species spawn in summer. They lay eggs in gelatinous or slimy clutches, which in *Limapontia cocksi* contain up to 30 large yellow eggs (diameter of an egg up to 160-200 mcm) and have a shape of semitransparent globular sacs. An egg is enclosed in a transparent capsule (a large axis of the capsule is up to 400 mcm, a small one up to 300 mcm). Clutches are attached to the bases of the filamentous algae and are not seen from the outside. Large (up to 15 mm in length), white, transparent, slimy botuliform clutches of *Alderia modesta* are attached openly, usually some clutches in a row, to the particles of ground or to filamentous algae with a slimy pedicle which reaches 1/3 of the clutch length; in water, they have a vertical position. The clutch contains some hundreds of small white eggs (egg diameter up to 80.2 mcm). One to two, sometimes three to four, and even nine eggs are enclosed in a capsule (large axis of the capsule containing one egg - 169.5 mcm, small one - 143.4 mcm). Egg cords inside the clutch are twisted into an incomplete spiral. Clutches of *Limapontia depressa* are botuliform, have a horizontal position on the ground, are attached to the substratum with their whole surface, the pedicle is missing, the length is up to 6 mm. The transparent membrane encloses the dense rows of several hundreds of small lemon-yellow eggs and the whole clutch looks yellow. The average diameter of the egg is 70.7 mcm. Usually one to two but sometimes five eggs are enclosed in a transparent capsule (large axis of the capsule containing one egg is 134.0 mcm, small one is 112.3 mcm). The clutches of *L. capitata* so resemble those of *L. depressa* that they can be identified only by means of a biotope (Hartog, 1958). In intertidal pits of Dalnie Zelentsy where single *L. capitata* were found with abundant *L. cocksi*, the clutches of the former have not yet been found, although it is known (Gascoigne, 1956) that the molluscs lay them in the same way as *L. cocksi*, i.e., at the bases of the bushes of *Cladophora*.

The development of *Limapontia capitata, L. depressa* and *Alderia modesta* has a stage of veliger with a spirally twisted larval shell. The whole embryonic development of *L. cocksi* occurs inside the membranes of the clutch, the larval shell does not develop, and young get out from the stroma differing from the adults only in size (Roginskaya, 1975). During its development, the larva accumulates the seeds of black pigment, which is clearly seen through a semitransparent membrane of the clutch; that is why, under field conditions, it is easy to define visually the degree of maturity of embryos. Veligers of *A. modesta* and *L. depressa* also accumulate black pigment during their development though in smaller amount as compared to *L. cocksi*. Seeds of the pigment are concentrated in a shape of black contour around the mouth opening, black granules in the anal gland and in the base of cilia on the velum. In this case, too, the black pigment is clearly seen through the membranes of the clutch, which looks greyish and differs visually from the white or yellow early clutches of these species.

All four species of Saccoglossa are boreal, intertidal species (Lemche, 1941), i.e., being eurythermic, at their vegetative phase they require a relatively high temperature for their reproduction. In general, these intertidal molluscs are distributed in boreal waters of Europe but could penetrate the Barents Sea (one species could even penetrate the intracontinental White Sea), where they found the necessary high temperature (during low tide higher than 20°) in the summer months in intertidal and supratidal zones. Of the four species, *Limapontia cocksi*, the life cycle of which has no pelagic stage, has certain advantages. The young of this mollusc just after emergence from the clutch gets to a suitable substratum and has an opportunity to begin feeding. That is why *L. cocksi* is distributed throughout the intertidal zone of both the Barents and White seas.

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THE ROLE OF THE BIVALVIA IN THE BENTHOS ON CONTINENTAL SHELVES WITH DIFFERENT PRODUCTIVITIES OF WATER

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Abstract

Bivalve molluscs are one of the most important benthic group on continental shelves; it defines the pattern of most bottom communities.

On shelves washed by highly productive waters (subpolar or tropical), bivalve molluscs occur practically in all stations. Depending on the mobility of demersal waters and the type of bottom deposit, the communities of bivalve molluscs of different trophic types develop: on stones and sands – sestonophags; on silty grounds – collecting detritophags. Within the limits of shelves washed with productive waters (eutrophic regions), the rows of parallel communities (according to Thorson, 1958) can be recognized. On shelves washed with low productive waters (oligotrophic regions), bivalve molluscs occur approximately in 50% of the stations and, regardless of the character of the ground, are represented exclusively by sestonophags. Communities of oligotrophic regions cannot be compared with any community of eutrophic regions; for oligotrophic regions of the shelves, their own system of parallel communities should be worked out.

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SOME ASPECTS OF THE LINEAR GROWTH OF BIVALVE MOLLUSCS IN A POPULATION OF *CERASTODERMA EDULE BELGICUM*

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Abstract

In August-September of 1973, when conducting a quantitative investigation of macrobenthos in the intertidal bank of Dalny Pljazh (the Dalne-Zelenetskaya Inlet, the Barents Sea), an abrupt increase in the number of *Cerastoderma edule belgicum* (de Malzine) was recorded. In the following years, the spat settlement did not take place and, up to the summer of 1976, when a mass mortality of these molluscs was observed, a stable population of animals of the same age existed here. It was estimated that every year the cockles form only one distinct winter ring on the shell. Additional or "disturbance ring" does not appear even after strong damages of the mantle edge of the shell. This has enabled the author to analyse some peculiarities of group and individual growth of *C. edule*. These peculiarities appear to hold for many other bivalve molluscs.

The growth of *Cerastoderma edule* is close to an isometric one. This is proved by a significant correlation between length (l) and height (h) – +0.99; length and width (b) – +0.97; height and width of the shell – +0.98. Habitual indices (h/b, b/l, b/h) are constant enough during the life of molluscs and variation coefficient of each of them does not exceed 5%.

Within each age group of the cockles, the size-frequency distribution conforms to the Gauss' one with high confidence ($P \geqslant 0.999$) and individual variability of linear measures of molluscs is high enough. For the first and second age groups, variation coefficient of the shell length accounts for 27 and 18%, respectively; then it decreased up to 10-15% and remained on this level irrespective of age. One of the factors affecting the decrease of individual variability with age is the mortality of larger individuals.

Reproduction is not followed by noticeable fall in growth rate. This regularity appears to hold, also, for all marine intertidal bivalves from the Barents Sea, which have a plancton larval stage, since their main energetic expenditures for the gonads' development take place in the winter-spring period, i.e., coincide with a period of winter growth stoppage. The shell length of *Cerastoderma edule* by the end of the growth season is in direct relation to the initial size.

Average values of shell length of molluscs of all contiguous age groups differ with confidence from each other. With an increase in age, however, the transgression of successive size-frequency distributions increases abruptly. Thus, the transgression index for the first and second age groups is 0.007 (7%), for the second and third groups it rises to 0.397 (39.7%) and for the third and fourth groups to 0.876 (87.6%). That is why, using such distributions as a criterion of age determination or life span of bivalves, one can, as a rule, distinguish the first age group ($P = 0.999$), to differ two- and three-year-old individuals ($P = 0.95$). Confidence of such statistical estimation decreases abruptly with the increasing life span of molluscs. If the recruitment occurs every year and the period of larva settlement is extended, the analysis of size-frequency distribution of such a population can turn out to be utterly useless, even in a separation of second and third age groups. For a definition of individual growth rates, it is preferable to use the area of first annual increment in relation to the area of the shell of the yearling.

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SOME ASPECTS OF THE ECOLOGY AND GROWTH OF THE SCALLOP *CHLAMYS ISLANDICA* IN THE BARENTS SEA

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Abstract

In order to solve the problem of the fishery use of the scallop *Chlamys islandica* (Müller), its distribution and ecology in the Barents Sea were studied.

The scallop is widely distributed in the Barents Sea and forms stable colonies in eight regions connected with zones of increased hydrodynamic activity of water masses. Colonies of the mollusc are located on the slopes of banks and trenches; temperature of water varies here from -1 to 3°C, salinity from 34 to 35‰ and oxygen content from 80 to 100%. The mollusc gives preference to depths of 50 to 200 m, sandy and muddy-sandy grounds with an admixture of empty shells. The most important factor affecting the distribution of scallops in marine aquatoria is the availability of constant near-bottom and descending currents carrying many organic remains, which serve as the main food for the mollusc.

Data on the quantitative distribution of the scallop in the Barents Sea were obtained for three regions. On the slopes of Gusinaya and Medvezhinskaya banks, in the bottom assemblage *Balanus balanus - Chlamys islandica - Alcyonidium gelatinosum* (Linnaeus) - *Strongylocentrotus droebachiensis* (Müller), the average biomass of molluscs was 100-150 g/m^2 at the density of 4-5 specimens/m^2. In inlets of East and West Murman coast, in the assemblage *Modiolus modiolus* (Linnaeus) - *Chlamys islandica*, the biomass of the scallop is 200-400 g/m^2 and density is 10-15 specimens/m^2. Here molluscs having a shell height over 60-70 mm make the main share of trawl catches.

The life span of the scallop (judged by the growth layers of shells and ligaments) off the coasts of East Murman does not exceed 15 years. The maturity sets in when molluscs are three to four years old; in younger age groups, males (over 60%) gain dominance and, in older groups (molluscs are five to seven years old), females (over 60%) gain dominance. The ratio between sexes is close to 1.

The linear and weight growths were approximated by the parabolic and S-shaped curves, respectively. The height of the largest specimens was 125 mm and weight was 300 g. The examined populations were represented, in general, by six to eight-year-old individuals with a shell height of 80-95 mm and weight of 85-110 g. A share of shell weight in relation to the total raw weight decreases from 55% in year-old individuals and to 39-32% in molluscs over seven years. The muscle weight in one year-old scallops amounts to 36% of raw weight of soft parts of the body, in two to four year-old molluscs to 45-50% and in older ones to 15-20%. A share of gonad weight varies from 2-8%, depending on the stage of maturity and the age of the mollusc. The elongation of the shell in height decreases with age. The ratio H/L in one-year-old molluscs is 1.21; beginning from the age of five years, the shells of molluscs become almost round (H/L = 1.02). The convexity of the shell rises with age. The ratio B/H in yearlings is 0.25, in four-year-old individuals it is 0.29, and in older ones, 0.31. Young molluscs have equally convex valves; beginning from the age of four to five years, the upper valve becomes more convex as compared to the lower ones.

On the whole, the growth rate of the scallop is much lower than in such fishery pectinids as *Patinopecten yessoensis* (Jay), *Placopecten magellanicus* (Gmelin) and *Aequipecten irradians* (Deshayes). High density and biomass of this mollusc in the places of its aggregation, however, allow us to hope that this species also will be able to become a fishery object on condition of its sufficient stock and strictly limited catch.

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PECULIARITIES OF THE ECOLOGY OF ABUNDANT BIVALVE MOLLUSCS FROM THE CHUPA INLET

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Abstract

Life cycles of 10 bivalve molluscs common to the intertidal and upper subtidal zones of the White Sea were studied. They are as follows: *Mytilus edulis* Linnaeus, *Mya arenaria* Linnaeus, *Macoma baltica* (Linnaeus), *Musculus discors* (Linnaeus), *Musculus laevigatus* (Gray), *Tridonta borealis* (Schumacher), *Nicania montagui* (Hancock), *Astarte elliptica* (Brown), *Hiatella arctica* (Linnaeus), *Heteranomia squamula* (Linnaeus). Their reproductive cycles, growth, distribution at depths, seasonal dynamics of the abundance and bioenergetic properties of populations and communities were analysed.

According to their geographic distribution, the species in question are, to a certain extent, boreal forms. Species which are capable of living in the intertidal zone (*Mytilus edulis, Mya arenaria, Macoma baltica*) have the greatest densities of communities and biomass in the middle and lower horizons of the intertidal zone and upper (to 5-8 m) subtidal zone, with *M. edulis* being dominant. Most other species have abundant communities in the zone of *Laminaria* distribution at depths from 2-3 m to 10-12 m. The molluscs *Tridonta borealis, Nicania montagui* and *Heteranomia squamula* have large communities at depths of 20-25 m.

The life cycles of molluscs from the coastal areas of the Chupa Inlet are characterized by a number of common features that is a result of their common origin and peculiarities of the temperature regime of the aquatoria. It has been established that the above species have a summer period of reproduction that is clearly seen in *Mytilus edulis, Mya aenaria, Macoma baltica, Hiatella arctica* and *Heteranomia squamula*, which have a pelagic larva in their ontogenesis. For *Mytilus, Mya* and *Macoma*, a surface water temperature of 10°C is a signal to begin mass spawning,

which occurs early in May. Differences in the periods of maturation of gonads in individuals of these species from different habitats are insignificant and practically do not affect the spawning in the Chupa Inlet. Identity in temperatures and spawning periods for the molluscs in question can be explained by the proximity of specific reproduction temperatures, short hydrological summer, considerable differences between winter and summer temperatures and common habitats. The species investigated become mature in one to two years at a size amounting to 30-50% of maximum ones. All the molluscs are characterized by an elimination of young in winter (from 53% in *Macoma baltica* to 95% in *Mytilus edulis* and *Hiatella arctica*) and relatively high growth rate. The latter phenomenon is associated with a very warm hydrological summer. The life span of molluscs varies by insignificantly and is from two to three years in *Musculus laevigatus* and *Nicania montagui* to seven to eight years in *Mytilus edulis* and *Mya arenaria*. Only single individuals of these species attain maximum age. This defines to a great extent a very young composition of communities and populations of molluscs in the Chupa Inlet. Apparently, just these circumstances explain their high bioenergetic indices ($K_2 = 0.33$; $P/B = 3$), which, to a great extent, depend on the age structure of communities and populations of molluscs.

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STUDIES OF BIVALVE MOLLUSCS AT THE INSTITUTE OF MARINE BIOLOGY

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Abstract

Bivalve molluscs are a rather convenient object for research in various branches of biology. This is due to a number of circumstances: a relatively good taxonomic investigation, slow mobility of many species, rather great abundance, variety of organization, ecology and functional characteristics in different genera and species and a presence of a number of unique objects especially suitable for certain investigations. In the Institute of Marine Biology, bivalve molluscs are investigated from various points of view in 10 laboratories and four structural groups.

As basic objects of investigation, certain mass species (some of them are commercial) are chosen; they are *Crenomytilus grayanus* (Dunker), *Mytilus edulis* Linnaeus, *Crassostrea gigas* (Thunberg), *Patinopecten yessoensis* (Jay), *Swiftopecten swifti* (Bernardi) and *Spisula sachalinensis* Schrenck). Hydrobiologists study composition and distribution of bivalves in the intertidal and upper sublittoral zones of the Soviet Far-eastern seas, as well as on the coral reefs of the West Pacific.

The works of ecologists are devoted to temperature and salinity adaptations of bivalve molluscs, their attitude to different grounds, anthropogenic effects and relations in biocenoses. Gametogenesis, embryogenesis and postnatal development are actively investigated, the special attention being paid to molluscan growth dynamics. Paleoecologists study a change of complexes of molluscs in the geological age, as well as the problems of stability and variability of attitude of one and the same molluscan species to environmental conditions. A development of ways for determining the absolute age of a number of bivalve species makes it possible to investigate the population age structure, formation of populations in time and questions of a change of sex in ontogenesis.

Cytologists have found peculiarities in the ways of cellular reproduction in various molluscs and studied hystophysiology of neurosecretion in some species. Biochemists, together with ecologists, physiologists and electron microscopists, elucidate mechanisms of various types of contraction in muscles of molluscs different in systematic position and life conditions. Population structure of species, questions of their evolution and biogeography, behavior and conditioned reflexes are studied.

Many of the mentioned works have an importance for practice. Molluscs were used as food as far back as by ancient people. The special work of our scientists is devoted to this object and is made together with anthropologists from Vladivostock. In accordance with the special orders of TINRO (Pacific Institute of Fisheries and Oceanography) and Dalziba (Far-eastern Board of Fishery Industry), the scientists of the Institute of Marine Biology made a series of researches connected with the population structure, study of ecology, ontogenesis and growth regularities of the main mariculture objects: scallops, oysters and mussels. The role of bivalves in fouling and dependence of larval settlement on the substrate are studied in detail. The investigation of molluscan reaction to anthropogenic effects and to the contamination with Cu, in particular, has been started.

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INVESTIGATIONS ON THE INDIVIDUAL GROWTH OF MARINE BIVALVES

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Abstract

Most studies of the marine animals growth were conducted by means of analysis of size or mass relations of simultaneously collected animals of the same age (method of "transverse section"). As a result, characteristics of their group growth were obtained. Individual growth of animals has been given little attention until now, although significant differences between growth curves of an individual and those of a group of animals were noted by many authors.

The presence of age marks in a shape of external growth rings or periodical elements in many species of marine bivalves, which are found on sections of various parts of the shell, gives an opportunity to use a method of reverse

calculation of growth rates of a single individual. If a valve is taken for a registrating structure, then there is no necessity to estimate preliminarily the relation between size of a structure and that of an individual to define annual increase in growth or size of a mollusc. In this case, the accuracy of definition of linear growth indices depends only on the accuracy of measurements.

In most marine molluscs, the life span is over a year and curves of their annual increment are quite enough to analyze the regularities of their individual growth. Each curve can be represented as a sum of three main components which characterize age changes, annual rhythms and occasional variations in growth rates.

Age changes in growth rate usually have three stages: juvenile, adult and senile. Some molluscs (*Mytilus edulis* Linnaeus, *Mercenaria mercenaria* (Linnaeus)) lower their linear increments that also can be seen on the group growth curves. In some other species, the transition from the juvenile stage to adult one proceeds gradually; empiric curves, as in a case of group growth, are well determined by Bertalanffy's growth equation.

The senile stage of growth is not so well studied. In *Modiolus modiolus* (Linnaeus), *M. difficilis* (Kuroda & Habe), *Crenomytilus grayanus* (Dunker), *Mercenaria mercenaria*, *M. stimpsoni* (Gould), *Cyclocardia crebriocostata* (Krause) and some other molluscs, the linear growth abruptly slows down when reaching a definite size or age and the edges of the shell become blunt on account of primary growth of valves only in thickness. As a result, a character of some allometric relations changes, and for a description of this section of the empiric growth curve another equation is required. In some molluscs (*Glycymeris yessoensis* (Sowerby), *Spisula sachalinensis* (Schrenck), *Peronidia zyonoensis* (Hatai & Nistyama), *Mya japonica* Jay, etc.), differences between the character of linear growth at adult and senile stages are not so sharp, but for their description it is better to use different equations.

Investigations of individual age changes in the mollusc's mass are quite laborious. In this case, curves of average, annual calcification rate, i.e., annual increment of valve thickness at its outer surface, can serve as indirect indices of such changes. Using *Crenomytilus grayanus*, it has been established that while passing to a senile growth stage changes in this parameter, in contrast to increments of the shell in height or length, do not alter the character of dependence on age and are described by the same Bertalanffy's equation as at the preceding stage.

On the background of age decelerations, long-term variations in growth rate manifest themselves. They account for 40 to 200% of the normal increment and represent rhythms of different order. In molluscs with a longer life span (*Crenomytilus grayanus*), there were found intracentinal changes in calcification rate. They are characterized by a slow growth of animals in 1855-75, 1920-40 and are apparently associated with global climatic changes. Smaller rhythms with a period of 3-4, 5-7, 10-13 and 20-24 years have a smaller amplitude of variations and are rather synchronous in individuals of the same species from different regions.

Long-term rhythms can also manifest themselves in the individual growth of molluscs with a life span less than 10 years (*Acila insignis* (Gould), *Clinocardium californiense* (Deshayes), *Septifer keenae* Nomura, etc.). In this case, on each curve one or two bends are seen which can be taken for the borders of growth stages. To distinguish such accelerations or decelerations in growth rates from age rates is possible only by analyzing long rows of observations or measurements. It should be noted that the transition to a senile growth stage is connected with conditions unfavorable for growth.

Variations in growth rate, which are not synchronous in value in different individuals, are considered as occasional ones. Apparently, they also are determined, but a concrete cause of such changes in growth rate in most cases remains unknown. Very rarely a sharp decrease in annual increment can be associated with such unfavorable effects as boring the shell by predators, injuries of valve edges and getting ground particles into the mantle, which are reflected in the outer and inner structure of the shell.

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SOME ASPECTS OF OYSTER REPRODUCTION

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Abstract

In oysters of the genus *Crassostrea*, sex can change within their life in the period of indifferent condition of the gonad; during the reproduction season, oysters of this genus are dioecious and do not change sex. Members of the genus *Ostrea* change sex, as a rule, repeatedly during the reproduction season. Oysters of the genus *Crassostrea* belong to species with alternating sex and oysters of the genus *Ostrea* belong to species with a successive rhythmical change of sex. A polygenous definition of sex in oysters of the genus *Crassostrea* is suggested.

Both genera are characterized, in general, by protandry. Among oysters of the genus *Crassostrea*, functional hermaphrodites occur rarely, as compared to the genus *Ostrea*.

Gametogenesis in both genera proceeds in a similar way. Spermatogenesis is completed in the testis. In *Ostrea*, spermatozoids are formed in special capsules in which they are ejected into water. There are no such capsules in *Crassostrea*. Meiosis in females' gonads does not complete fully and continues when oocytes get into the water after fertilization. Seasonal changes in gonads of oysters are different in members of two genera. The reproductive cycle of *Crassostrea* is characterized by only one gametogenetic cycle. Within a year, *Ostrea* can have several gametogenetic cycles separated from each other by a short stage of rest. The reproductive cycle of both genera has an indifferent stage which is characterized by a reduction of gonad and lack of differentiated reproductive cells. The growth of gonad and gametogenesis proceed simultaneously and each process characterizes the reproductive condition of an individual.

The growth and maturation of reproductive cells in oysters are affected by environmental conditions. Under experimental conditions at an increased temperature, when food requirements are satisfied, the development of gametes

takes several days. Estradiol 17β causes an accelerated maturation of gametes and transformation of the male sex of the individual into a female one. Temperature, food and other environmental factors synchronize the state of the population before spawning. Species of *Crassostrea* eject eggs directly into water, i.e., are oviparous (not incubatory) species unlike larviparous (incubatory) *Ostrea*. Momentary abrupt effect of one or some main factors can be a direct stimulator of a spawning reaction of oysters. Specific substances of oysters secreted into water during spawning cause an analogous effect.

A reproduction period in *Ostrea* is longer than that in *Crassostrea* that is associated with a sex change in this period. Among members of *Crassostrea*, the gigantic oyster *C. gigas* (Thunberg) has the shortest spawning period. The duration of a reproduction season of some species of oysters is affected by a geographic localization of its populations. The run of the spawning season depends on the structure of populations of a species. Each population of oysters of the same species is physiologically adapted to environmental conditions and responds in a different way to their changes. This is expressed in temperature differences affecting the beginning of spawning and the duration of the spawning period. The assumption of the existence of physiological races in oysters must be subjected to an accurate genetic analysis.

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ECOLOGICAL AND MORPHOLOGICAL FEATURES OF THE PACIFIC OYSTER *CRASSOSTREA GIGAS* FROM NATURAL AND CULTIVATED POPULATIONS IN THE BAY OF PETER THE GREAT

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Abstract

Materials on ecology and morphology of Pacific oysters were obtained in 1975-77 when studying their populational structure in Possiet and Amur bays and when studying oysters cultivated by an experimental marine base of Far-Eastern Technical Service of Fisheries in Novgorod Inlet (Possiet Bay). Ten natural populations and three cultivated generations were investigated. Linear, weight and volume parameters as well as their ratios and indices were studied. Seasonal changes of these parameters in one natural and cultivated populations were observed.

According to the main morphological characters (shape of the shell, linear, weight and volume ratios), three principal groups of populations adapted to definite environmental conditions are arranged.

The first group includes populations from the mouth of Lebiazhja Lagoon and from lagoons connected with Expedition Bay. This region is characterized by powerful intertidal currents, abruptly decreasing salinity of water and by abundant suspended particles. Temperature of water in summer can be 30°C. The oysters here form dense aggregations in the shape of brushes. The ratio between the length and height of the shell is less than 0.4, the ratio between the width and height is less than 0.2, and the ratio between the volume of the shell and the total volume is in the range of 0.5 to 0.6.

The second group includes the population of oysters from closed shallow bays where salinity of water is from 18 to 32°/oo. In these regions, the values of most factors of the environment are close to optimal for the Pacific oyster. Populations of oysters off Chikhachev, Rjazanov, Shelekh and Kurgan capes can serve as an example. The ratio between length and height is, on the average, 0.4 to 0.5, between width and height is 0.20 to 0.27 and between volume of the shell and total volume is 0.45 to 0.55.

The third group includes populations of oysters from open and semiclosed bays and intertidal oysters off islands and exposed capes. The regions are characterized by a constantly increased salinity of water (about 30-34°/oo), decreased temperature of water in summer (20-23°C) and by a great wave effect. Populations of oysters from Vitjaz and Minonasok inlets, near Afanasiev Cape and Furugelm's Island, are an example. The ratio between the length and height is over 0.6, between width and height is 0.27 to 0.40, on the average, and between the volume of the shell and the total volume is 0.55 to 0.65.

Oysters cultivated in the Novgorod inlet occupy and intermediate position between the second and third group in their morphological indices. The ratio between the length and height varies from 0.6 to 0.7, between width and height from 0.2 to 0.3, and between volume of the shell and total volume from 0.4 to 0.5. In cultivated oysters, mass and volume of the shell in relation to the total mass and volume are correspondingly less than in oysters of natural populations, and mass of meat is greater.

Before spawning, a relative mass of the shell falls or keeps on a constant level, while during spawning it increases considerably. In the second half of summer, a relative mass of the oyster's shell falls, e.g., in cultivated oysters it decreases, on the average, from 64% in July to 53% in November. During spawning, the volume of the inner cavity of the shell decreases on account of the increasing volume of the shell, and after the end of spawning the volume of the shell cavity increases. At the same time, an increase in the share of soft body in relation to the total mass of mollusc takes place – in cultivated oysters from 7.7-16.8% and in oysters from natural populations from 4.7-6.8%. In cultivated oysters the commercial quality is higher, too.

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MORPHOLOGY AND POPULATION STRUCTURE OF THE BIVALVE *PATINOPECTEN YESSOENSIS* IN THE SOVIET FAR EAST

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Abstract

In 1975, the population structure and morphology of the bivalve mollusc *Patinopecten yessoensis* Jay from the

Far East and Sakhalin were studied by the standard techniques. The evaluation of phenotypes was conducted according to electrophoretic mobility of fractions of the liver esterase (Bogdanov, Bregman & Flusova, 1977) and evaluation of the habitus of populations was conducted by the method of identification of patterns (Andreev & Bregman, 1977) and by studying the character of frequency distribution of values of some indices.

Due to inconstancy of annual replenishment, the size-age structure of investigated aggregations is of irregular character. Populations from Zapadnaja Inlet (Furugelm's Island) and Lake Vtoroje (Gulf of Nakhodka), where scallops of all generations occur, are most different in age and are heterogenous morphologically.

The sex ratio is close to 1; in most samples, hermaphrodites were found (three to five specimens per 1000). Reproductive part of the populations in open bays and inlets, Halovey, Zapadnaja, Melkovodnaja, Preobrazhenia inlets, Olga Bay, accounts for 93-99%, in isolated inlets such as Andreev's Inlet and Lake Vtoroje for 88% and 59%, respectively.

According to the character of age variability of some morphological indices, the investigated samples can be arranged into two groups: Zapadnaja, Halovey, Andreev's inlets, Schkot's Island; Melkovodnaja and Preobrazhenia inlets, Lake Vtoroje, Olga Bay. In Scallops of the first group, the relative depth of the lower shell is considerably smaller; relative mass of the muscle increases with age, reaches its maximum and then decreases. It remains two — 1.2 times higher than a nearly constant value of this index in scallops of the second group; relative mass of the upper valve remains constant; in scallops of the other group it decreases with age. The frequency distribution values (united into two samples) of the indices in question are in accordance with the described-above pattern; curves of the distribution differ with confidence in their parameters.

Scallops from Bousset Lagoon (Sakhalin) have a special type of habitus. Biochemical polymorphism in locus I corresponds on the whole to morphological differences of the samples. Some samples differ with confidence in frequences of the mobility type C (Lake Vtoroje - Zapadnaja Inlet; Olga Bay - Andreev's Inlet; Lake Vtoroje - Schlot's Island; Melkovodnaja Inlet - Andreev's Inlet).

As to the samples from Zapadnaja Inlet and Bousset Lagoon, the distribution of genotypes with confidence $p>99\%$ does not correspond to the low of Hardy-Weinberg: in the first case heterozygotes CD gain dominance; in the second, homozygotes CC. The scallops from the Far East are characterized by the D type of mobility and those from Sakhalin by the C type. The E type was observed but with rare frequency (0.01-0.05), only northwards from Andreev's Inlet and in scallops occurring off Sakhalin.

Two hypotheses were advanced. They explain the lack of confident differences by the empiric and theoretical distribution of genotypes of most samples. Two other hypotheses consider the causes of disbalance of genotypes in samples from Zapadnaja Inlet and Bousset Lagoon.

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PERIODICITY OF GROWTH AND REPRODUCTION IN THE CASPIAN BIVALVE *DIDACNA TRIGONOIDES*

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Abstract

Data on the growth rate of *Didacna trigonoides* (Pallas) were obtained. Molluscs were reared in cages installed on the bottom of the northern Caspian Sea in different months.

Age groups were distinguished and their seasonal linear and weight growth was studied. Most intensive growth in all seasons was observed in yearlings. The linear growth of two to three-year-old molluscs is arrested in spring (April) and renews again in the second half of the summer (July). A pause in growth of four-year-old and older molluscs lasts during the whole warm period of the year.

Pauses in the linear growth of older age groups are, apparently, a result of reproduction which takes place in May and June. This agrees with data on the continuous growth of yearlings, which do not spawn at this time. After spawning, the gonad is in a state of full devastation; interfollicular tissue is practically missing. A curve of weight growth shows a considerable (to 50%) fall in the mollusc's body weight, which is connected with an ejection of sexual products by the end of the spawning season. Renewal of interfollicular tissue, which serves for accumulation and storing of the reserve nutrients, continues till October and then a new cycle of gametogenesis begins. Renewal of linear growth in two to three-year-old molluscs proceeds till the full completion of these processes. In older individuals the growth period begins later, only after the completion of the regeneration period (October).

At the cold time from the end of October to April, considerable linear and weight growth of individuals of all age groups was observed. This growth is supposed to occur, in general, late in autumn (November) and early in spring (March, a part of April), at a water temperature from 5-10°C.

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PECULIARITIES OF THE TEUTHOFAUNA (CEPHALOPODA, OEGOPSIDA) FROM ANTARCTIC WATERS

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Abstract

The present report is based on the material collected during Antarctic cruises on board the scientific fishery vessels "Academic Knipovich" and "Professor Mesjatsev" (1965-76) and on investigations of the feeding of sperm whales conducted on board the whale-fishing flotilla "Sovetskaya Ukraina" (1969-76).

In the limits of the Antarctic region, i.e., throughout the aquatoria limited from the north by the Antarctic convergence zone, 19 species of squids belonging to 16 genera and 11 families of the suborder Oegopsida were found.

The Antarctic teuthofauna includes relatively many monotypic genera (*Psychroteuthis, Alluroteuthis, Batoteuthis, Parateuthis, Mesonychoteuthis*) and a smaller number of families. Only two families, Onychoteuthidae and Cranchiidae, are represented more diversely. A sufficient part of species presents forms which can be regarded as relict and relatively primitive.

Teuthofauna of the Antarctic is characterized by a high degree of endemism. The genera *Psychroteuthis, Alluroteuthis, Kondakovia, Mesonychoteuthis* and *Batoteuthis*, and the species *Moroteuthis knipovitchi*, can be considered endemics. In addition to endemics, the teuthofauna includes notal Antarctic elements (*Gonatus antarcticus* Lönnberg, *Moroteuthis ingens* (Smith) and *Histioteuthis eltaninae* Voss) and widely distributed ones (*Taonius pavo* (Le Sueur) and *Bathyteuthis abyssicola* Hoyle).

The fact that Antarctic teuthofauna includes a great number of endemics of high rank and that it largely consists of relict and primitive forms point to an ancient and long existence of the Antarctic basin. This conclusion agrees with that of Andrijashev (1965) concerning the ichthyofauna of Antarctica.

Brachioteuthis (? *riisei* (Steenstrup)) is the most abundant form of the upper horizons of pelagial in this region. In mesopelagial and upper horizons of bathypelagial, large members of the families Onychoteuthidae (genera *Moroteuthis* and *Kondakovia*) and Cranchiidae (*Mesonychoteuthis hamiltoni* Robson) dominate. In bathypelagial, *Bathyteuthis abyssicola* is most abundant.

Being qualitatively poor as compared to the teuthofauna of the neighboring region, the fauna of squids from the Antarctic region is characterized by the availability of forms forming large aggregations.

As investigations on the feeding of sperm whales have shown, the most abundant squid in high latitudes is the deep-water Antarctic species *Mesonychoteuthis hamiltoni*. It amounts to 60% of the diet of these whales. Its biomass in the limits of the Antarctic region amounts to approximately 60 million tons. Large squids of Onychoteuthidae hold the second place in their significance.

Antarctic squids can be referred to two trophic groupings of different levels: a) zooplankton phags or krillophags (consuments of the second order, the third trophic level); b) predators, living on account of small swarm fishes and squids (consuments of the third order, the fourth trophic level).

Taking into consideration the great abundance of squids in the Antarctic region, their large size and the fact that they are the main food object of many Antarctic vertebrates, that they themselves consume a great amount of krill, small swarm fishes and other squids, it should be admitted that they play an important part in the ecosystem of the Antarctic region, affecting all its links.

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FEEDING AND HELMINTH FAUNA OF THE DEMERSAL SQUID *DORYTEUTHIS SINGHALENSIS* IN THE WESTERN PART OF THE INDIAN OCEAN

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Abstract

Collections of the squid *Doryteuthis singhalensis* (Ortmann) conducted in December 1976 off the south-eastern slope of the Mascarene underwater ridge, which is characterized by rather heterogenous ecological conditions, have served as material for this report.

As a result of the analysis of the vertical distribution, size-weight composition, the degree of maturity of gonads (1500 specimens) and feeding (100 specimens), it has been revealed that the population of *Doryteuthis singhalensis* in this region inhabits depths up to 220 m and is represented by two sympatric groupings.

Most abundant groupings (74% of investigated individuals) live throughout the whole region. Sizes of squids are from 6-21 cm. The range of sizes of maturing males and females is 8-21 and 10-17 cm, respectively. The coefficient of fatness decreases with increasing size from 2.37 to 1.03% in males and from 2.86 to 1.20% in females.

The second grouping lives only in the northern part of the region. Sizes of squids are from 6-23 cm. Males become mature when reaching a size of 10-23 cm and females when reaching 11-17 cm. The coefficient of fatness varies from 2.22 to 0.51% in males and from 1.87 to 0.59% in females.

Analysis of food spectrum of squids has enabled us to distinguish main, secondary and occasional food objects for the first grouping and only main food objects for the second one. This affects the coefficient of diversity of food: in the first case it amount to 2.53; in the second, to 1.64.

Doryteuthis singhalensis is an attacking type of predator. Both groupings consume fish (78% according to occurrence and 40% according to weight), crustaceans (80% and 28%), squids (11% and 32%) and Chaetognatha (42% and 0%). In squids belonging to the first grouping, the secondary food objects are copepods (*Oncaea* and *Pareuchaeta*), amphipods (Fronimidae) and stomatopods; the occasional food objects are isopods, ostracods and Tunicata.

The content of most main food components of squids of the first and second groupings changed in ontogenesis. Only a share of euphausiids in ration of individuals of different size groups remains nearly the same. In two of 100 squids of the first grouping (12.6 and 13.0 cm in size), there were found in the stomach cavity larvae of nematodes of the genus *Spinitectus*, the definitive hosts of which are teleost fishes.

From our point of view, the formation of two sympatric groupings of squids of *Doryteuthis singhalensis* is stipulated by heterogenous ecological conditions on the south-eastern slope of the Mascarene underwater ridge.

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ADAPTATIONS OF NUTRITION AND RESPIRATION OF MOLLUSC EMBRYOS

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Abstract

Reproduction of molluscs is connected with an elaboration of a whole number of adaptive characters associated with nutrition and respiration of a developing embryo. One of the adaptations to a supply of embryos with nutrient material is an availability of protein fluid in cocoons or embryonic capsules. From the early stages of development, embryos of molluscs actively consume protein and its amount gradually decreases with the growth of embryos. The amount of protein in egg clusters of molluses, which differ ecologically in their developmental type, is quite diverse.

The initial concentration of protein in eggs of *Helix pomatia* Linnaeus accounts, on the average, for 14%. Eggs are laid into peculiar nests dug in the ground and lined inside with mucus. Each cluster contains, on the average, 32 eggs (the diameter of an egg is about 7 mm, weight is about 125 mg). Their development at room temperature lasts about three weeks.

The initial content of protein in eggs of *Planorbarius corneus* (Linnaeus) is about 7.3%. Eggs are small, about 1 mm in size; they are laid in cocoons united into clusters. The number of eggs in the cluster is 71, on the average. At room temperature, the development is over in 11-13 days. Concentration of protein in a nutritive fluid falls to 1.2-2.3% before the emergence of young.

The initial content of protein in embryonic capsules of *Viviparus viviparus* (Linnaeus) is 4-7 times higher than that in *Helix pomatia*. It is possible that such a great amount of protein is characteristic of *V. viviparus* because it is a viviparous form, providing an embryo with optimal conditions of nutrition inside the maternal organism. In addition, under certain conditions, the development of embryos can last for months, and this requires high amounts of protein and nutritive fluid.

A low amount of protein in a nutritive fluid of eggs of *Planorbarius corneus* may be due to the fact that young molluscs when emerging from an egg weigh only about 1 mg, ie., 3-4 thousand times less than a maternal individual. Newborn molluscs of two other species are only 4-6 times lighter than adults.

The protein fluid of eggs of investigated molluscs differs in its consistency and color. In *Viviparus viviparus* it is blue, viscous and opaque; in *Helix pomatia* it resembles protein of a hen's egg and is colorless; and in *Planorbarius corneus* the fluid is pink, liquid and transparent. The differences in consistency of the nutritive fluid are easily explained by the amount of protein in it. Its color may depend on the presence of respiratory proteins characteristic of hemolymph of an adult: hemocyanin in *V. viviparus* and hemoglobin in *P. corneus*.

Viviparus viviparus has a number of morphological characters that facilitate the respiration for embryos. Walls of the mollusc's uterus contain a net of blood vessels, are lined with ciliate epithelium and make wave-like motions, thus assisting the mixing of the fluid between embryonic capsules and facilitating gas exchange.

Observations have shown that in *Planorbarius corneus* there is a dependence between the content of oxygen dissolved in water, the color intensity, the number of clutches and the number of eggs in them. According to preliminary data, a low concentration of oxygen results in a decrease in the number of eggs and egg clusters and in a rise of the intensity of pink color of nutritive fluid.

Motion of embryos by means of numerous cilia mixing the protein fluid creates better conditions for their nutrition and respiration inside eggs.

Different developmental periods of eggs and different time of emergence of the young are characteristic features of all investigated molluscs. This is an adaptive character for optimal survival of young during the transition to an independent mode of life.

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THE RATE OF GROWTH AND METABOLISM OF THE FRESHWATER SNAIL *BITHYNIA TENTACULATA*

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Abstract

A study of such ecological and physiological indices as growth rate and oxygen consumption intensity during the respiration of *Bithynia tentaculata* (Linnaeus) is of great interest from both the general biological and practical points of view.

Experiments on growth and respiration of *Bithynia* were conducted in the summer of 1973 to 1974 in the Kremenchug water reservoir. The molluscs grew in cages installed on the bank of the reservoir, in three parallel series, each series containing several tens of individuals. Observations on the weight and linear increment were conducted each 10 days.

The oxygen consumption rate was studied by the method of closed bottles with a determination of oxygen dissolved in water according to Winkler's method. Bottles with experimental animals were placed in one great vessel containing water from the reservoir. Temperature of water in experiments was usually 20-24°C. When temperature of water deviated from 20°C, a corresponding correction according to "normal curve of Krogh" was made.

The duration of exposition of bottles was 3-5 hrs. Animals collected in the reservoir just before the beginning of the experiment were used for experiments. In all calculations, the author used the total raw weight of molluscs, including the weight of the shell, soft body and liquid of the mantle cavity.

Observations on the growth of *Bithynia* were started from young 2.4 mm in length and 3 mg in weight. Molluscs

grew, in general, 39 days and, at the end of observations, reached 8.6 mm in length and 97 mg in weight, thus increasing their linear sizes 3.5 times and weight 36 times for this period. According to the experimental data, empiric curves of the linear and weight growth of *Bithynia* were plotted, which reflect the character of its growth for 39 days.

Since regularities of weight growth connected in a direct way with regularities of metabolism are of great interest, the empiric curve of weight growth was subjected to particular analysis. The curve was divided into sections corresponding to short periods of time (three days), and for each section an average specific growth rate was calculated.

$$C_w = \frac{\lg W_2 - \lg W_1}{(t_2 - t_1) \cdot 0.4343} \qquad (1)$$

According to obtained data, the specific growth rate of *Bithynia* decreases with increasing weight. At the initial stage of growth (the first three-day interval), the specific growth rate was very high (about 49% per one day). During the next three-day interval, it decreases to 17.5% for a day, etc., and at the end of observations was 1.8% per day. On the average, during the period of observations, the specific growth rate of *Bithynia* accounted for 8.9% per day.

In experiments conducted by Arabina (1971), the growth rate of *Bithynia* was much lower (0.26-3.25%, or on the average about 2% per day). Such low growth rate of molluscs is, apparently, due to lower temperature of water during experiments. In the experiments conducted by the author, molluscs grew at a temperature of 20.3-23.9°C or, on the average, at 22.5°C. According to the data of Arabina, the average temperature of water in the lake was 16.5°C, with an amplitude of fluctuations from 11.2-21.6°C. It is clear that such differences in conditions of growth could not but affect its rate.

In experiments on oxygen consumption rate, a wide size-weight group of animals was used, *viz.* from 0.0027 to 0.207 g. Results of observations are expressed in ml O_2/spec./hr. On the basis of these data, it should be noted that the quantity of consumed oxygen per a unit of time regularly increases with increasing weight of mollusc. If molluscs from the lowest weight group (average weight of an individual was 2.7 mg) consumes 0.00039 ml O_2/spec./hr, then the oldest individuals (average weight, 207 mg) consume 0.0102 ml O_2/spec., i.e., an increase in oxygen consumption by one individual was of over 20 fold. As to metabolism intensity, it should be noted that in this case just the reverse tendency is observed, i.e., with increasing weight of a mollusc, its respiration rate decreases from 0.186 ml O_2/g. hr in individuals of 4.4 mg in weight to 0.042 ml O_2/g. hr in animals of 146 mg in weight. Thus, data on the oxygen consumption by *Bithynia* confirm the general regularity on the decrease in metabolism intensity with increasing weight of animals and with a simultaneous increase in its rate.

Thus, the dependence of metabolism rate of *Bithynia* on weight can be expressed by the equation

$$R = 0.036.W^{0.725} + 0.035 \qquad (2)$$

where R = the quantity of oxygen consumed by an individual, ml/hr, and W = weight of an animal, g.

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PECULIARITIES OF THE BIOLOGY OF THE MOLLUSC *MELANOPSIS PRAEMORSA MINGRELICA*

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Abstract

Vast studies are being carried out now on the parasite fauna of the freshwater mollusc *Melanopsis praemorsa mingrelica* Issel at the Department of Invertebrate Zoology of Leningrad State University (Olenev & Sobrovolsky, 1975; Galaktionov, 1976; Olenev, 1976; Tikhomirov, 1976; etc.). This mollusc, which occurs in the Soviet Union only in western Georgia (Shadin, 1952; Starobogatov, 1970; etc.), is a unique intermediate host of trematodes. Parthenites of 27 species of flukes were found in it. Of special interest are investigations connected with a study of host-parasite relationships between molluscs and parasitic and free-living stages of flukes. It is clear that such studies are impossible without knowledge of biology of the intermediate host itself. At the same time it should be admitted that in the available zoological literature such data are missing.

Small rivers with silty grounds serve as habitats for *Melanopsis praemorsa mingrelica*. As a rule, these waterbodies do not exceed 3-5 m in width and 50-100 cm in depth in summer. Often the bed of such a river passes on the bottom of a shallow canyon with thick bushes and trees along the shores where even on bright sunny days there is little light. Current velocity varies from several centimeters per minute at the shore to 80,100 cm/sec at the rapids.

Mostly the mollusc keeps near the shore at a shallow depth. Its aggregations are observed in areas abounding with food, fallen leaves in general. These are, primarily, leaves of elm, oak and maple. In such places, molluscs can form large aggregations up to several hundreds and thousands of individuals. Though molluscs occur more often in sunlit areas, there was observed no distinct correlation between presence of these animals and lighted places. The molluscs are rather mobile and can migrate for considerable distances (up to 20 m and over).

The behavior of molluscs in response to the effect of different environmental factors was studied experimentally. It has been shown that illumination gradient does not play any significant part in the distribution of the molluscs throughout the aquarium. At the same time, experiments have shown that the molluscs prefer zones with a temperature 10-15°C higher than the normal one. Apparently, a certain unevenness in the distribution of molluscs in nature (sunlit and shady areas) is associated with just this factor. Aggregations of the molluscs in shallow, warmed backwaters result from the motion of animals along the increasing temperature gradient rather than from their reaction to the light.

A study of the vertical distribution of molluscs has shown that the animals have a tendency to aggregate on the surface at the water level. Now we cannot explain the causes that make molluscs move to the upper layers. Very

possibly it is a result of negative geotaxis. Vertical orientation of the mollusc's body during its lift speaks in favor of this supposition. The main factor, however, that makes molluscs migrate upwards is, apparently, the oxygen deficiency in the near bottom part of the body of water.

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THE LATE CRETACEOUS MOLLUSCS OF MONGOLIA

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Abstract

The territory of Central Asia, and of Mongolia in particular, represents a vast region where the freshwater malacofauna developed as far back as Mesozoic times. Many of the bivalves and gastropods later spread widely in the river and lake systems of Siberia, Kazakhstan and Middle Asia.

Most abundant and interesting complexes of molluscs were found in continental deposits of the Late Cretaceous in South Mongolia. In these biocoenoses, peculiar, large and costated bivalves of the superfamily Trigonioidoidea are prevalent. Unionids are represented not so widely. Gastropods are represented by various Viviparidae, Bithyniidae, Ampullariidae and Valvatidae.

Representatives of trigonioidoids are known only from the deposits of the Asiatic Continent. They occur in Japan, China, Indochina, Mongolia, Kazakhstan and Middle Asia. Cretaceous (internal basins of Central Asia) is known to be the most flourishing period of this group.

Numerous collections of fossil shells of this group from South Mongolia enabled the author to erect a number of new families. The superfamily Trigonioidoidea includes three families: Trigonioididae, Pseudohyriidae and Sainshandiidae, the first family being characteristic of Early Cretaceous, the second and third families of Late Cretaceous.

Of gastropods, most typical are sinistral shells of the genus *Mesolanistes* of the family Ampullariidae and members of the families Hydrobiidae and Viviparidae. These molluscs inhabited various biotopes of large internal basins of Central Asia under conditions of subtropical climate.

Vast collection material enabled the author to work out the taxonomy of freshwater molluscs of Central Asia and to trace the ways of their evolution.

At the demarcation of Late Cretaceous and Paleogene, most molluscs in Central Asia became extinct as a result of the reduction of vast lake systems and a change in climate. Only members of unionids and some gastropods have been preserved.

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THE MAIN RESULTS OF THE STUDY ON FRESHWATER PALEOGENE GASTROPODA IN KAZAKHSTAN

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Abstract

Successive complexes of molluscs, including gastropods, distinguished during the past 20 years in northwestern (Maderny, 1974), northeastern (Prutskaya, 1958), southeastern (Tolstikova, 1976), central and south-southeastern Kazakhstan have made it possible to carry out a comparative analysis of gastropods and reveal regularities of their changes in time and space.

In the Paleogene and the Neogene, changes in the composition of genera and families occurred more or less smoothly, but at the demarcation of these two systems the generic and specific variety greatly increased.

While in the Paleogene species with a narrow distribution prevailed, in the Neogene widely distributed species, the existence of which was limited by this period, gained dominance and the number of species living increased. Maximum specific variety of gastropods was in the Miocene, while in the Pliocene gastropod complexes became more and more monotonous.

The spatial distribution of gastropods stipulated by climatic and landscape factors is different in the Paleogene and Neogene. Most ancient complexes are reported from Zaisan Depression (Paleocene, Eocene and later), from Turgai Depression (Oligocene), and beginning from the Miocene from the whole territory which became free from the regressing sea.

Zoogeographic structure of freshwater gastropods for different regions of Kazakhstan was diverse to some extent during the Paleogene and Neogene. In the territory with a constant continental regime, in Zaisan Depression (now East Kazakhstan zoogeographic province), there was a connection with molluscs of the souther lake-river system. That is why gastropods are represented only by Asiatic thermophilous species. Beginning from the end of the Oligocene, the connection with southern regions was interrupted but exchange with molluscs from northern regions of Kazakhstan enlarged. In addition to Asiatic endemic species, Euroasiatic ones appeared.

Over the territory of northwestern and northeastern Kazakhstan (Irtysh zoogeographic province now), where repeated changes of the continental regime by the transgressing sea took place, endemic forms were prevalent in the Oligocene. In the Miocene, when the sea retreated finally, European immigrants and, to a lesser extent, Asiatic ones appeared among gastropods.

In central and south-southeastern Kazakhstan, which is distinguished now into Balkhash zoogeographic province, Asiatic elements were prevalent in the Neogene, while European elements played a subordinate part. By the end of the Neogene, the correlation between elements became nearly balanced. Thus, in the Paleogene and Neogene, Irtysh, East Kazakhstan and Balkhash provinces were distinguished by the difference in the composition of gastropods and by the specificity of physical and geographic conditions (Starobogatov, 1970).

In Irtysh province, in the Paleogene and Neogene, Vivipariidae were always present; in East Kazakhstan province, Bithyniidae; and, in Balkhash province, freshwater Pulmonata. Unlike the first two provinces, Viviparidae were not found in the latter.

Material collected in Kazakhstan gave start to a study of opercula of bithyniids, which occur in continental deposits more often than shells themselves. Their abundance, wide distribution, stratigraphic connection and morphological specificity determine their stratigraphic value.

Further investigations of freshwater gastropods from Kazakhstan must be directed at the more precise definition of generic and specific composition, at the revealing of their individual and group variability, at the possible phylogenetic relationships between species and ecological peculiarities.

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THE HISTORY OF NON-MARINE BIVALVES IN THE NORTHERN CISURALIAN DURING THE PERMIAN PERIOD

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Abstract

About 90 species of non-marine bivalves are known from Permian deposits of the Northern Cisuralian (Pogorevich, 1956, 1977; Gusev & Muravjev, 1962; Kanev, 1972, 1977; Gusev, 1977). They belong to eight genera and five families as follows: Palaeomutelidae (*Palaeomutela*), Prilukiellidae (*Prilukiella*), Anthracosiidae (*Anthraconaia*), Abiellidae (*Abiella, Concinnella, Mrassiella*), Anthraconautidae (=*Myalinidae*, in part) (*Anthraconauta, Sinomya*). These bivalves existed in the Northern Cisuralian approximately from the middle of the Kungurian to the Tatarian age inclusive and characterize here the Permian period in the development of the Bivalvia fauna. Particular substages in the development of non-marine bivalves correspond to each geological age of the Late Permian period. These substages are characterized by a renewal of the specific and to some extent of generic composition of bivalves, but genetic relations are preserved between them due to long-living species and continuity of some genera.

In the Kungurian age in the Northern Cisuralian, non-marine bivalves first appear in the Vorkuta region and are represented here by numerous species of the genus *Sinomya* and by single species of *Pelaeomutela, Anthraconauta* and *Concinnella*.

In the Ufan age, non-marine bivalves are widely distributed in the Northern Cisuralian and, at the same time, members of the genera *Anthraconaia, Anthraconauta, Mrassiella* and *Abiella* gain mass development. Interrelations between late Kungurian and Ufan developmental substages are accomplished through *Pelaeomutela, Anthraconauta* and *Concinnella*. Some species of *Anthraconauta* and *Abiella* appeared in the Ufan age and continued to exist in the Kazanian age. At the boundary of the Ufan and Kazanian ages, a renovation of the specific composition of *Palaeomutela, Anthraconauta* and *Concinnella* takes place but *Anthraconaia* and *Mrassiella* disappear.

In the Kazanian age in the region of the Middle Pechora, an outbreak of speciation in *Palaeomutela* took place, and here members of the genus *Prilukiella* and *Sinomya*-shaped forms, which, apparently, are a new subgenus of *Sinomya*, appear. In more northern regions, *Anthraconauta, Concinnella* and *Abiella* become most abundant and some species of *Anthraconauta* and *Abiella* continue to exist in the Tatarian age. By the end of the Kazanian age, *Palaeomutela* and *Sinomya* either migrate from this territory or become fully extinct.

The Tatarian developmental substage of non-marine bivalves is characterized by a renovation of the specific composition of *Prilukiella, Concinnella, Abiella* and *Anthraconauta* and by the appearance of members of the subgenus *Procopievskia*. In the Tatarian age, these bivalves become especially abundant in the basins of the Adzva and Korotaikha rivers.

On the boundary of the Permian and Triassic in the Northern Cisuralian, the disappearance of all Permian non-marine bivalves takes place that is a kind of manifestation of the Permian peak of extinction of families and genera of bivalves. This is associated with a fundamental paleogeographic reconstruction of the territory in question at the end of the Permian period.

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THE HISTORY OF THE FORMATION OF THE LAND AND FRESHWATER MOLLUSCAN FAUNA IN THE EASTERN PART OF THE TRANSCAUCASIAN UPLAND

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Abstract

In the eastern part of the Transcaucasian Upland, 157 species of molluscs occur. The history of the formation of of this fauna can be traced by means of paleogeographical data and by means of the information of paleofaunas of neighboring countries.

Beginning from the Devonian, there was a great island here, almost a flat, poorly elevated plain. In the Jurassic, the crushing of the earth's crust and wrinkling began and this process continued in the Cretaceous and later. Approximately in the middle of the Late Cretaceous (Santonian), a continuous stretch of land with a monotonous climate of tropical savannas appeared here. This area extended from southern Europe through Asia Minor, Transcaucasian, northern Iran to southern Turkmenia. Thus, opportunities arose for a migration of Cretaceous European fauna into Transcaucasian and further to the East. At that time, the fauna already included all Recent families of freshwater molluscs and members of nearly all subfamilies of land molluscs. At the same time, ancestors of the endemic family Trigonochlamydidae appeared here. In the Late Cretaceous (Campanian), Transcaucasian underwent the strongest sea transgression in its history: here there was an open sea nearly without islands. Some parts of the former land, however, were preserved in the neighborhood. When, before the very beginning of the Cenozoic, there was a new raising of land, which turned Transcaucasian into the archipelago of islands with mountains of average height, these islands became inhabited again. The climatic zonality remained the same as it was before the transgression but the mountains became covered with forests. By this time in Europe, a number of Recent land families already existed and they could appear in Transcaucasian. In the Paleocene, the land connections with Europe were broken. This favored the rise of endemic nidi of the fauna formation in Asia Anterior and in the Caucasus. The islands of the Great Caucasus were covered with tropical forests, but in the mountains they were replaced by subtropical forests. In Transcaucasian, on the plains, there were steppes and savannas, while in the mountains there also were forests. Just at this time, there arose distinct Caucasian and Transcaucasian faunas.

In Eocene, a new transgression of the sea into Transcaucasian occurred that divided this region into two groups of islands: western and eastern. The western islands were adjacent to the land of northern Anatolia and the eastern islands to northern Iran. The connection between East and West was resumed again only in the Upper Eocene and broken off again in the Oligocene. Thus, conditions arose for a separate formation of Minor Asiatic and North Iranian faunas.

In the Early and Middle Oligocene, sea left the middle latitude zone of the eastern part of the upland. Bending by the axis of this zone was formed and in this place a large freshwater lake arose which stretched from Dilizhan to Turkey. There are findings of our most ancient molluscs from this region: *Hydrobia, Melanopsis, Lymnaea, Helix*; all of them now are extinct species. In the Late Oligocene, the raising spread throughout the whole country. The sea retreated, leaving large lagoons which separated the country as before. In its northern part, a subtropical humid climate prevailed, and southwards of this watershed was a tropical arid climate of savannas and steppes. Thus, there were created conditions for the formation of two nidi of mesophilous fauna, northwestern Somkhet and northeastern Karabakh, and two nidi of xerophilous fauna, southwestern Armenian and southeastern Atropatenian. This explains the generic endemism of these nidi, since it is known that the process of the formation of Recent genera of land molluscs was completed on the whole in the Oligocene.

In the Middle Miocene (Konkian), a new sea transgression occurred. Through the narrow bay along the Agstev river, the sea came up to the town of Razdan. Here, in marine coastal deposits, a Recent freshwater species of *Melanopsis* and two fossil species of xerophilous land molluscs referred to the genus *Zebrina* were found. In the Late Miocene, the subtropical climate spread throughout the whole country and a land connection with southern Europe, where the same climate prevailed, was resotred. It was the time of the appearance in Transcaucasian of a new immigration of widely distributed European and Aegean species, including Recent ones, which at that time already inhabited southeastern Europe. The eastern part of the country had direct land connections with the south through Syria and Arabia, with the east through Iran to the Asiatic land, and in the north of the western part of the country with the Great Caucasus. In large, sometimes freshened lagoons, Recent genera but extinct species lived.

In the Early Pliocene (Meotian), the sea left definitely Anterior Asia and Transcaucasian. The junction of the western and eastern parts of the country caused some countermigrations of the fauna. In northern parts of the country, there was climate of the current mediterranean type. The same climate continued westward to South Europe and eastward to the Kopetdag Mountains along vast parts of land.

In the southern part of the country, the climate was close to a temperate one or subtropical savanna-steppes. This climate existed throughout the territory from western parts of internal Anatolia to northeastern Iran. In the mountains the climate was less warm. It can be suggested that most Recent species already existed there. According to the data on Europe and North Caucasus, the process of formation of Recent land species was completed, in general, in the Meotian. In the Middle Pliocene (Pontian), in Transcaucasian, local raising occurred: at that time, Aragats, Gegam and other mountains appeared. Their feet, however, were not very high above sea level. At the same time, the Great Caucasus joined with the land of the European part of the U.S.S.R. and Caucasian isthmus arose. Northwards from Great Caucasus there existed a wide zone of quite another climate, a steppe zone, which hindered the migration of the faunas. In the Late Pliocene (Akchagylian, Apsheronian), along the periphery of mountain formations, there existed numerous lakes in which Recent species lived together with those which are extinct now.

In the Early Pleistocene (before the Bakuan Age) and in the Middle Pleistocene (before the Khazarian), there were two phases of the general raising of the whole country and thus the recent high-mountain relief was formed. In the Bakuan Age, the cooling increase in humidity, spreading of forests (even coniferous forests at the end of the age in the north) occurred. At that time, conditions were created for migration from the north of the widely distributed and Caucasian species which live in this region now, not lower than the upper forest zone. At Pre-Khazarian time, relatively warm and dry conditions prevailed; steppe and, in the south, desert vegetation was spread. At that time Atropatenian species, which later had gaps between their areals and main habitats, spread to the north. In Khazarian and Khvalynian ages, the country underwent two mountain glaciations: glaciers covered the whole Karsk plateau, northeastern corner of Armenia and many mountain tops. In Transcaucasian at that time appeared Siberian, high mountain Caucasian and north Iranian species. Thermophilous fauna was concentrated in shelters on lower levels. And, at last, in the Holocene there were formed recent conditions of the fauna existence.

FIRST RESULTS OF RESEARCH ON PLIOCENE AND PLEISTOCENE LAND MOLLUSCS IN THE DON DRAINAGE AREA

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Abstract

The drainage area of the Upper Don is the only territory in the central part of the Russian plain where vast collections of Pliocene molluscs were conducted. Large amounts of material were obtained from Lower, Middle and Upper Pleistocene deposits. As regards the European part of the U.S.S.R., Pliocenian land molluscs were known primarily from the Black Sea and Uralian areas.

Material was obtained during geological investigations by washing clay and sand through a net with a cell diameter of 0.8 mm. Geological age was determined on the remains of small mammals found in the same deposits. Pliocene molluscs were found in six sites.

A small but rather diverse Middle Pliocenian fauna of Antipovka consists primarily of extinct thermophilous species. Here were found six species of the genus *Gastrocopta* (Pupillidae *sensu lato*).

The Upper Pliocene (Middle Akchagylian) faunas of Uryv and Korotojak are rich in specimens and species and differ greatly from each other ecologically. The fauna of Korotojak consists of over 10 species of land molluscs, including *Gastrocopta acuminata* Klein, *G. nouletiana* Dupuy, *G. magna* Steklov and *G. pseudotheeli* Steklov. Many shells were found of a new species belonging to the American subgenus *Vertigopsis*. This subgenus is recorded for the first time in Neogenian deposits in the U.S.S.R. Fragments of shells and intact sinistral shells of the genus *Chondrula* were found in great abundance. They belong, apparently, to some undescribed species. The species *Vertigo antivertigo* Draparnaud, which is missing in Korotojak, is the most abundant in the fauna of Uryv. Shells belonging to the American subgenus *Angustula* were found. The genus *Gastrocopta* is represented only by the subgenus *Vertigopsis*. Fragments of shells belonging to the Mediterranean genus *Parmacella* are present.

The Apsheron fauna of Gorianka consists primarily of Recent species but contains a number of extinct ones, including sinistral *Chondrula, Gastrocopta nouletiana, G. (Vertigopsis)* sp. nov. and *Vertigo (Angustula)* sp. nov.

Cold-loving elements appear in early Pleisticenian faunas. From this time, repeated alterations took place of thermophilous faunas containing primarily Recent European species and cold-loving faunas containing extinct species or those very rare for the Russian plains, which are characteristic representatives of "loess" complex: *Vallonia tenuilabris* Braun, *Vertigo parcedentata* (Sandberger), *Pupilla sterri* (Voith) and *Columella columella* Martens.

Very rich and diverse Middle Pleistocene (Odintzovo?) fauna of Strelitza nearly does not contain extinct species. In the Upper Quaternary (Mikulinian) site of Pavlovka (Tambov district), there were found thermophilous molluscs, including *Gastrocopta nouletiana* and *G. theeli* (Westerlund).

In the State reserve Galichja Gora (Lipetsk district), on lime rocks together with numerous Pleistocene relict plants, lives *Pupilla sterri*, which is also a Pleistocene relict.

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MOLLUSCS IN THE SPRINGS OF ESTONIA

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Abstract

On the basis of 350 samples collected in 1955-57, the fauna of molluscs from 78 springs of Estonia (56 springs of the northern part and 22 of the southern part) have been analysed. Molluscs occurred in 60% of the springs examined.

The fauna of springs has turned out to be much poorer than that of lakes and rivers. Here, 22 species were found as follows: *Viviparus contectus* (Millet), *Lymnaea auricularia* (Linnaeus), *L. lagotis* (Schranck), *L. patula* (Da Costa), *L. ovata* (Draparnaud), *L. intermedia* (Lamarck), *L. stagnalis* (Linnaeus), *L. atra* (Schranck), *L. fontinalis* Studer, *L. mucronata* Held, *Anisus contortus* (Linnaeus), *A. vortex* (Linnaeus), *Planorbis planorbis* (Linnaeus), *Ancylus fluviatilis* Müller, *Pisidium amnicum* (Müller), *Euglesa splendens* (Baudon), *E. ponderosa* (Stelfox), *E. tenuisculpta* Pirogov & Starobogatov, *E. pulchella* (Jenner), *E. henslowana* (Sheppard), *E. fossarina* (Clessin) and *E. humerosa* Pirogov & Starobogatov.

Most abundant and diverse fauna (19 species) is recorded from large springs of the Silurian plateau in northern Estonia, especially in its karst parts. Only nine species were recorded from southern Estonia.

Most abundant and frequently occurring in the springs are *Euglesa fossarina, Lymnaea auricularia* and *E. humerosa*.

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THE ECOLOGY OF BIVALVES IN THE EASTERN PART OF THE BALTIC SEA

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Abstract

Material on the ecology of bivalves was collected by the author in 1959-76. The area investigated includes the

whole Gulf of Riga and Straits of Muhu (=Väinameri), the Gulf of Finland (except Neva Bay, Vyborg Bay and the territorial waters of Finland), the Baltic Proper southwards as far as Klaipeda and westwards as far as the medial of the Eastern Gotland Basin. Two thousand one hundred and twenty-five samples of bottom fauna from 1150 stations were examined, including 1455 qualitative samples taken by a bottom sampler from more than 900 stations.

Mytilus edulis Linnaeus. Marine low arctic-panboreal species with amphiboreal distribution; sessile sestonophag. In the Gulf of Finland, the species occurs up to the line: Lökskär Island-Hogland Island (=Suursaari)-village Valaste. Found at a depth of 0.1-89 m, at a temperature of 0.3-20.8°C, salinity of 3.9-9.5°/oo and minimum concentration of O_2 of 1.3 ml/l. Bathymetric optimum in Straits of Muhu is 0-10 m, in the Gulf of Riga it is 0-30 m, and in the central Baltic is 10-30 m. Absent from those parts where in the spring salinity is lower than 3.5°/oo. Lithophilous species. On fine-grained grounds the mollusk attaches to macrophytes and empty mollusk shells; prefers biotopes with intensive dynamics of water masses. Most abundant in α-mesosaprobic zone of polluted areas. The population density is up to 60,360 specimens/m^2 and biomass is up to 3,117 g/m^2.

Dreissena polymorpha (Pallas). Brackish-water neolimnical panboreal species of Caspian origin; sessile sestonophag. In the eastern Baltic the species was recorded from the Kurish Bay (Gasiunas, 1959) and sublittoral of the Gulf of Riga. For some climatic reasons it does not occur in the Baltic Sea northwards of the Pärnu Bay. It was found in the Gulf of Riga at a depth of 0.5-12 m, in summer at a temperature of 6.8-22.7°C and salinity of 3.5-6.0°/oo. Bathymetric optimum is 2-5 m. Lithophilous species. The population density is up to 100 spec/m^2 and biomass is up to 23.5 g/m^2.

Cerastoderma lamarcki (Reeve). Brackish-water panboreal eastern Atlantic and Sarmatian species; vagil sestonophag. In the Gulf of Finland, it is distributed eastwards up to the line of village Pernaja-village Saka. Found at a depth of 0.1-27 m, at a temperature of 0.3-25.3°C and salinity of 3.4-7.3°/oo. Bathymetric optimum in the central Baltic and Gulf of Finland is 0-5 m, in the Gulf of Riga and Straits of Muhu 0-10 m. Euryedaphic species. Occurs frequently in great number on silty grounds with hydrogen sulphide smell. Most abundant in shallow semiclosed bays. α-β-mesosaprobic species. The population density is up to 17,840 spec/m^2 and biomass is up to 200.7 g/m^2.

Macoma baltica (Linnaeus). Marine panboreal species with amphiboreal distribution; collecting detritophag. In the Gulf of Finland, it occurs up to the line Berezov Islands-Island Seskar (=Seiskari)-Petrodvorets (Knipovich, 1909; Schlesch, 1937; Suomalainen, 1939). Found at a depth of 0.2-88 m, at a temperature of 0.3-21.4°C, salinity of 2.2-10.8°/oo and minimum concentration of O_2 lower than 1 ml/l. Bathymetric optimum in the Gulf of Riga is 1-30 m, in the Gulf of Finland 1-40 m, in the central Baltic 1-60 m; occurs in places in great abundance up to a depth of 70-80 m. Summer temperature optimum is very wide - from 2-20°C. Salinity optimum in the Gulf of Riga and Straits of Muhu is 3.5-7.5°/oo, in the Gulf of Finland 3-9°/oo and in the central Baltic 6-10°/oo. Euryedaphic species. Most characteristic species of zoobenthos in the eastern Baltic; dominates in its biomass almost throughout the whole area. Its absence from the vast moderately deep parts of the Gulf of Finland is due to the eating of its young by Arctic relict crustaceans *Pontoporeia affinis, P. femorata* and *Mesidotea entomon*, together with detritus. Most abundant in α-mesosaprobic zone of polluted areas. Population density is up to 21,560 spec/m^2 and biomass is up to 437.6 g/m^2.

Mya arenaria Linnaeus. Marine panboreal species with amphiboreal distribution; vagile sestonophag. In the Gulf of Finland, the species occurs up to the line large village Sipoo-village Vainupää. Found at a depth of 0.2-35 m, at a temperature of 0.3-22.7°C and salinity of 3.5-8.6°/oo. Can withstand O_2 deficiency and hydrogen sulphide in bottom sediments. Bathymetric optimum in the Gulf of Riga is 2-10 m, and in the Gulf of Finland and the Straits of Muhu 2-15 m. Summer temperature optimum is 12-19°C and salinity optimum is 5.5-7.0°/oo. Euryedaphic species; its abundance depends on the amount of seston in near-bottom water. Most abundant in α- and β-mesosaprobic zones of polluted areas. Population density is up to 6,200 spec/m^2 and biomass is up to 1,097.3 g/m^2.

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ON BIVALVES OF THE FAMILY PISIDIIDAE AND THEIR PARASITES IN TATAR A.S.S.R.

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Abstract

Collections of molluscs were conducted from 1972-77 in various water bodies of the drainage area of the Middle Volga and the Lower Kama (the Volga-Kama State Reserve and vicinity of the city of Kazan). In all, 38 water bodies were examined, including lakes, lakes-bogs, branches, bays, old river beds, water bodies of the impoundment area, near-channel part of the Volga spur of the Kuibyshev water reservoir and the small forest river Ser-Bulak with its area of impoundment. Members of the family Pisidiidae were found in 16 water bodies.

The conducted investigations have enabled the authors to supplement the available data (Gromov, 1935; Kurbangalieva, 1957, 1965; Aristovskaya, 1958, 1960, 1964) on the Pisidiidae fauna of this region.

Thirty-seven species belonging to seven genera were found as follows: *Musculium ryckholti* (Normand), *M. creplani* (Dunker), *M. hungaricum* (Clessin), *M. mucronulatum* (Moquin-Tandon), *Amesoda scaldiana* (Normand), *A. draparnaldi* (Clessin), *A. solida* (Normand), *Sphaeriastrum rivicola* (Lamarck), *Sphaerium nucleus* (Studer), *S. nitidum* (Clessin in Westerlund), *S. corneum* (Linnaeus), *Pisidium amnicum* (Müller), *P. inflatum* (Muehlfeld in Porro), *Euglesa tetragona* (Normand), *E. obtusalis* (C. Pfeiffer), *E. solida* (Clessin in Westerlund), *E. dubrueili* (Baudon), *E. scholtzii* (Clessin), *E. nitida* (Jenyns), *E. fedderseni* (Westerlund), *E. subtruncata* (Malm), *E. turgida* (Clessin in Westerlund), *E. supina* (Schmidt), *Euglesa* sp. n. 1, *E. henslowana* (Sheppard), *E. volgensis* Pirogov & Starobogatov, *E. behningi* Pirogov & Starobogatov, *Euglesa* sp. n. 2, *Euglesa* sp. n. 3, *E. fossarina* (Clessin in Westerlund), *E. globularis* (Clessin in Westerlund), *E. curta* (Clessin), *E. acuminata* (Clessin in Westerlund), *E. obliquata* (Clessin), *E. pallida* (Clessin), *Euglesa* sp. n. 4 and *Neopisidium torquatum* (Stelfox).

We are most grateful to Dr. Y.I. Starobogatov of the Zoological Institute of the Academy of Sciences of the U.S.S.R. for his help in identification of molluscs.

Some species of molluscs display their associations with definite water bodies and their different parts. Most widely distributed are members of the genus *Sphaerium*, found in 11 water bodies. *Musculium creplini* and *Pisidium amnicum* occur more often than others. The first species was found in seven, the other in six water bodies. These molluscs have adapted to the life in lakes, bogs, the river and water reservoir.

As to *Euglesa*, it should be noted that despite their specific variety the molluscs were found only in eight water bodies and often only in ther definite parts to they occur in lakes, water bodies of the area of impoundment, the river and water reservoir. The density of *Euglesa* is high in silted parts of the Ser-Bulak and especially in aquatic vegetation of its impoundment area, where they amount to hundreds and thousands of specimens per 1 m^2 Here the greatest specific variety, 15 species, was recorded.

Four hundred and fifty-two specimens of *Sphaerium nitidum, S. corneum, Musculium mucronulatum, M. creplini, E. casertana*, and *Amesoda* sp. and *Euglesa* sp. not identified to species, collected in water bodies of the Reserve, were subjected to a parasitological study. Their total infection with larvae of trematodes was 4.2%.

In *Musculium creplini* and *M. mucronulatum* there were found cercariae of *Allocreadium isoporum* (Looss) (Allocreadiidae), in *Sphaerium corneum* were found *Gorgodera pagenstecheri* (Sinitzin) (Gorgoderidae), and in *Amesoda* sp. were found *Bunodera luciopercae* (Müller) (Bunoderidae). The definitive hosts of these parasites are fishes and amphibians. The infection extent is not high. In addition, in all examined species of pisidiids, there were found metacercariae of *Echinoparyphium echinatoides* Philippi (Echinostomatidae), the definitive hosts of which are domestic and wild waterfowl. The infection intensity is from one to 19 specimens.

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MALACOFAUNA OF THE FRESHWATER AVANDELTA OF THE VOLGA RIVER

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Abstract

At present, the Volga avandelta represents a large biotopically diverse region, the area of which is about 10 thousand km^2. It is mostly overgrown with semiaquatic and submerged vegetation. Grounds are primarily sandy with broken shells and silty to a certain extent. The current is discharging, weak, disturbed by wind-tide fluctuations. Most of the avandelta does not exceed 1 m in depth. Its northern part is rich in islands. The region is characterized by intensive dynamics of physical and geographical processes connected with economic activities of man (regulation of the Volga flow) and with natural processes expressed in secular fluctuations in the sea level and affecting considerably the bottom fauna state, the fauna of molluscs in particular.

In the 1920s of this century, the malacofauna of this region included mainly Dreissenidae, while other molluscs were small in number (Chugunov, 1923, and others).

In the 1960s, the regulation of the Volga flow, shallowing, redistribution of the biogenic flow and sedimentation resulted in considerable changes in the malacofauna composition. *Dreissena* was replaced by numerous members of the genus *Valvata*, Unionidae, Pisidiidae, etc. According to our investigations in 1968, we distinguished in this region nine complexes of molluscs which differed both in species composition and in quantitative relations. For example, the basis of the complex "dense *Typha-Phragmites* thickets of the islands of the northern part of the avandelta and silty-sand ground with numerous vegetable remains" was composed by such species as *Sphaerium nitidum* (Clessin in Westerlund), *Euglesa casertana* (Poli) and *Valvata cristata* Müller. The former, except for this region, was not recorded from the whole lower Volga (up to Volgograd) and the other species have a rather limited distribution in the delta. Together with them were recorded *Lymnaea danubialis* Schranck, *Planorbarius corneus* (Linnaeus), *Planorbis planorbis* (Linnaeus), *Anisus vorticulus* Troschel, *Hippeutis euphaea* (Bourguignat), *Physa fontinalis* (Linnaeus), etc. They do not live in the interinsular areas of the avandelta. The basis of the complex "sandy littoral zone" of these islands is composed by widely distributed *Valvata ambigua* Westerlund, *V. piscinalis* (Müller) (the abundance up to 3000 specimens/m^2; biomass up to 400 g/m^2) and *Anodonta cygnea* (Linnaeus) (the species which was recorded from nowhere besides this region). Together with this species, there were recorded *Viviparus viviparus duboisianus* Mousson, *Theodoxus pallasi* Lindholm, *Bithynia tentaculata* (Linnaeus), *Anisus acronicus* (Férussac), etc. The total abundance of molluscs in this complex accounted for 8000 spec/m^2 and biomass for 0.8-1.5 kg/m^2. In all, 57 species of molluscs were recorded from the region in question.

Changes in the bottom fauna are taking place now, too. Thus, the biotope sandy "littoral zone" of islands of the northern part of the avandelta disappeared and correspondingly changed the aspect of the malacological complex. The "littoral zone" virtually never becomes dry, the absolute level of water does not fall below 0.40 m and its aquatoria is grown with submerged vegetation (*Vallisneria* and others). The abundance of *Valvata* decreased up to 100-200 spec/m^2 (in 1977) but the number of lymnaeids increased. It was, apparently, due to the overgrowing of "marine bar" with thickets of exposed vegetation. A natural dam was thus formed, which created a lock up of water. In this area, the number of leading species of the complexes abruptly decreased (*Sphaerium nitidum* from 200-300 to 1-5 spec/m^2; *Valvata cristata* and *Euglesa casertana* were not found in 1977 at all).

A considerable part of the avandelta is occupied by shallow waters overgorwn with submerged aquatic vegetation (underwater meadows). It is especially characteristic of coastal areas of islands at 2-m depths (Chistaja Bank, Ukatny Islands) and of "marine bar". The abundance of molluscs here reached 5000-6000 spec/m^2. Earlier, the aquatoria of "underwater meadows" was rich in phytophilous species, *Valvata* spp., *Theodoxus pallasi, Viviparus viviparus*, etc. Now the malacofauna consists, in general, of lymnaeids. In coastal waters of the Chistaja Bank island, *Lymnaea fontinalis* Studer, *L. lagotis* Schrank and *L. stagnalis* (Linnaeus) reached 2600 spec/m^2, while the number of other species

was 500 spec/m^2. Here was recorded *Planorbis sieversi* Mousson, which had penetrated this area, apparently, due to freshening of the northern Caspian and was known earlier only from the delta of the Terek.

The state of the fauna in other regions has remained unchanged. Now in the area of the avandelta, very intensive geomorphological processes are occurring, and naturally great changes in the bottom fauna and, correspondingly, in the malacofauna are taking place.

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THE BIOTOPICAL DISTRIBUTION OF MOLLUSCS IN THE IRTYSH BAY OF THE BUKHTARMA WATER RESERVOIR

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Abstract

The Bukhtarma water reservoir was formed in 1960 as a result of the flooding of the Irtysh Bay (formerly Irtysh impoundment area) and Lake Zaisan with the delta of the Cherny Irtysh. The reservoir is of great energy and fishery importance. The Irtysh Bay unites the mountain-valley and mountain parts of the reservoir and is characterized by great depths, different thermic regimes and by not yet formed grounds.

The quantitative composition of benthos of the Irtysh Bay differs from that of the lake part of the reservoir. Changes in the distribution of molluscs are associated with the increase in depth in the longitudinal direction. In the Slaviansk region of the Bay, there were found such deep-water species as psammopelorheobiont *Pisidium amnicum* (Müller) (20-25 specimens/m^2), pelabiont *Valvata piscinalis* (Müller) (5-6 spec/m^2) and limnopelobionts *V. sibirica* Middendorff (8-10 spec/m^2) and *Euglesa securidens* Krivosheina (4-5 spec/m^2). Phytobiont *Hippeutis diaphanella* (Bourguignat) (1-2 spec/m^2), which occurs rarely with aquatic vegetation, is an exception.

Malacofauna of the Narym region, including the impoundment area of the Narym river, is characterized by a great variety of species. Phytobionts are represented by species of *Lymnaea*: *L. stagnalis* (Linnaeus), *L. peregra* (Müller), *L. auricularia* (Linnaeus). Among lymnaeids, thelmatobiont *L. saridalensis* Mozley (6-7 spec/m^2) occurs. The leading ecological group here is represented by limnopelobionts. Many of them, such as *Valvata sibirica* (9-11 spec/m^2), *Euglesa subcuneata* Krivosheina (3-4 spec/m^2) and *E. depressissima* Krivosheina (3-5 spec/m^2) are adapted to depths up to 20 m; some others, e.g., *Sphaerium nitidum* Westerlund (5-8 spec/m^2), *Musculium creplini* (Dunker) (2-3 spec/m^2), inhabit depths of 1-2 m. At depths to 8 m, there were psammorheobionts *V. ambigua* Westerlund (3-4 spec/m^2) and *Sphaerinova inflata* (Middendorff) (1-2 spec/m^2).

In deep waters (up to 40 m) of the Cheremshan region, the pelopsammatheobiont *Pisidium amnicum* is the most distributed and most abundant. It occurs together with the limnapelobiont *Valvata sibirica* (2-3 spec/m^2) at depths up to 20 m. At lesser depths (up to 10 m), rheophils live – pelarheobiont *V. piscinalis* (5-6 spec/m^2) and psammorheobiont *V. ambigua* (3-4 spec/m^2), *Euglesa montana* (1-2 spec/m^2) and *E. borealis* (8-10 spec/m^2). Phytobionts are small in number. In coastal waters of bays, only *Anisus acronicus* (Férussac) (7-8 spec/m^2) and *Armiger crista* (Linnaeus) (2-3 spec/m^2) occur.

The October region of the reservoir, which includes the impoundment areas of the Irtysh and Bukhtarma with a well-developed network of tributaries, is represented by parts that are different in morphometric respects, and so the composition of its malacofauna is heterogenous. The reophilous species *Pisidium amnicum* (30 spec/m^2) and *Valvata ambigua* (3-4 spec/m^2) are most abundant and occur at depths up to 10-15 m. The ecological grouping of limnopelobionts associated with silty grounds and rotting aquatic plants is very diverse.

In the Irtysh Bay of the reservoir, five reophilous and 13 species of limnopelobionts were found, species of the genus *Bithynia* being absent. According to the frequency of occurrence of reophilous species, the malacofauna of the Irtysh region of the reservoir is close to the fauna of the rivers' beds, while the presence of limnopelobionts makes it close to the malacofauna of lakes.

It is difficult to speak about the ecological groupings as about completely formed ones, since this part of the reservoir is young and the process of the fauna formation is still proceeding in it.

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EUROPEAN MALACOFAUNAL ELEMENTS IN THE LOWER PART OF THE YENISEI DRAINAGE AREA

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Abstract

The Recent fauna of most of Middle Siberia was formed, in general, in the Postglacial period. The Yenisei meridional faunistic border divides the northern Palaearctic into two large parts: European-West Siberian and East Siberian. The region in question belongs to the Lower Yenisei malacogeographical province of the East Siberian subregion of the Palaearctic (Starobogatov, 1970).

On the basis of the author's collections in 1973-77, there is a possibility of establishing the composition of freshwater molluscs of the family Lymnaeidae in the Lower Yenisei drainage area.

The 10 following species have been mentioned in the literature for the above region: *Lymnaea stagnalis* (Linnaeus), *L. fragilis* (Linnaeus), *L. auricularia* (Linnaeus), *L. torquilla* Westerlund, *L. intermedia* Michaud, *L. fontinalis* Studer, *L. atra* (Schranck), *L. terebra* (Westerlund), *L. truncatula* (Müller) and *L. sibirica* Westerlund. Thirteen additional species are first mentioned by the author for this region: *L. tumida* Held, *L. patula* Westerlund, *L. inflata* Kobelt, *L. ovata* Draparnaud, *L. ampullacea* Rossmässler, *L. intercisa* Lindholm, *L. palustris* (Müller), *L. glutinosa* (Müller), *L. zazurnensis* Mozley, *L. kurejkae* Gundrizer & Starobogatov, *L. dolgini* Gundrizer & Starobogatov, *L. igarkae* Gundrizer & Starobogatov and *L. dipkunensis* Gundrizer & Starobogatov.

The diversity of ecological conditions in different geographical zones gives a possibility for gastropods to exist in water bodies of different types – river-accessory, impounding, placoric. Twenty-two species of the above lymnaeids were recorded for the northern taiga zone and only seven of them (32%) for the drainage of the left bank tributary (the Turukhan River). On the whole, in the above zone, six species (27%) occur in river-accessory, 19 species (86.4%) in impounding and three species (13.6%) in placoric water bodies. In water bodies of the tundra zone, seven species of lymnaeids were found (four species in each type of water body). In the zone of forest-tundra, six species of lymnaeids were found (26.2% of the total number) only in impounding water bodies. Some lymnaeids occur simultaneously in three types of water bodies.

The greatest number of species was recorded from the drainage of the right bank tributary of the Kureika River in the zone of northern taiga. Such diversity of species was not reported even from East Siberia (drainage areas of the Olenek and Lena rivers).

The Yenisei malacofauna consists, in general, of species which have European-Siberian distribution, and the finding of new European elements points to the association of the malacofauna of the Lower Yenisei with that of West Siberia.

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COMPOSITION AND DISTRIBUTION PATTERNS OF THE MOLLUSCS IN THE ESTUARY OF THE AMUR

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Abstract

Hydrobiological collections in the estuary of the Amur (including Schastje Bay) were conducted by means of Petersen's bottom-sampler, 1/40 m^2, at 75 stations in July of 1971 and from June to September of 1972. In 1972, at the same time, plancton collections were carried out (middle type of Apschtein planctonic net) and salinity of water in surface and demersal layers was determined by argentometric technique. In all, 180 bottom samples and 140 plancton samples were taken. The occurrence frequency of molluscs accounted for 58% and that of their pelagic larvae accounted for 13%.

Malacofauna of the estuary of the Amur is represented by freshwater, brackishwater and marine euryhaline species. The distribution of freshwater species is limited by the estuary of the Amur and its neighboring parts. Freshwater complex of molluscs includes 17 species, of which *Valvata amurensis* Moskvicheva, *Sphaerinova limanica* Moskvicheva, *Euglesa corbiculaeformis* Moskvicheva, *Pisidium amurensis* Moskvicheva, *Amuropaludina chloantha* (Bourguignat) and *A. praerosa* (Gerstfeldt) are widely distributed. Main aggregations of molluscs are concentrated on silty grounds and in thickets of potamogetons, 1040-1280 specimens/m^2. The greatest biomass, 782-2283 g/m^2, was registered for molluscs of the genera *Amuropaludina* and *Juga*.

The freshwater complex of the Iski River (basin of the Schastje Bay) includes such widely distributed species as *Valvata amurensis, Euglesa corbiculaeformis, Pisidium amurensis*, and the pelostagnophils *E. memptunensis* Moskvicheva, *E. oblonga* Moskvicheva and *E. biraensis* Moskvicheva.

The brackishwater complex is represented by *Corbicula japonica* Prime and *Potamocorbula amurensis* (Schrenck). They occur primarily in the southern part of the estuary and are associated with waters of Japan origin.

Corbicula japonica was found at salinity of water from fresh to 6.2°/oo and its pelagic larvae was found in water from fresh to 1°/oo. They were found as well in the zone of contact of fresh and brackish waters. Small specimens with a mass from 9-84 mg were concentrated in freshwater. The sample taken on 22 July 1972 off Dzhaore Cape was an exception. The average mass of individuals from the sample was 1271 mg at the abundance of 1240 spec/m^2. In brackish water the mass of molluscs varied from 190-3592 mg. The largest individuals were recorded, in general, off Dzhaore Cape. Besides, on 30 August 1972, molluscs with mass of 1490 mg were found off Khalezovo Cape (Sakhalin). The main aggregations of this species occurred in the region of Dzhaore Cape-Uarke Cape-Chastye Islands. Corbiculids were found as well in the northwestern part of the estuary and in the eastern part of Schastje Bay. In August, the distribution of corbiculids extended up to Khalesovo Cape. Maximum density of molluscs was recorded in July (1210-1360 spec/m^2, biomass 1570-1500 g/m^2) and in September (1240 spec/m^2 and 390 mg/m^2).

The distribution of *Potamocorbula amurensis* is associated, in general, with salinity of water from 5-45°/oo or with the boundary of brackish and marine waters. Besides, from 6-21% of potamocorbulids (in relation to the number of individuals collected from a unit of the area) were found at the salinity of 5°/oo and from 1-11% were found in fresh water. In July and September, 77-93% of molluscs and nearly 100% of their pelagic larvae were recorded at salinity of 5-15°/oo. In August, bottom forms of potamocorbulids (up to 72%) were concentrated at salinity of 10-20°/oo and pelagic larvae (92%) at salinity of 5-10°/oo. This is associated with peculiarities of water exchange through the estuary of the Amur. In August or during monsoon hydrological period, a maximum distribution of

waters of Japanese origin takes place in the estuary that is accompanied by the increase in salinity of water. In July 1972, the salinity of the demersal layer in the eastern part of the estuary was 10-15°/oo, and in August it increased to 15-20°/oo. In September, when the Japanese waters retreated to the south, the salinity decreased to 0-5°/oo, but in the south of the estuary it still reached 5-15°/oo. Pelagic larvae of potamocorbulids were transferred with water to the freshened parts of the estuary, but the bottom forms of molluscs could not migrate for long distances within such a short period.

A connection between the distribution of young and adult potamocorbulids and salinity gradients was observed. Most molluscs concentrated at low salinity gradients (0.002-0.5°/oo/m). The second group of molluscs was adapted to gradients of 0.5-4.0°/oo/m. The same distribution also is characteristic of pelagic larvae, the main aggregations of which (80-93%) occurred at gradients of 0.002-0.5°/oo/m.

The maximum number of potamocorbulids was recorded in September in the southern part of the estuary – 4280 spec/m^2. In July, aggregations reached only 2980 spec/m^2, and in August the abundance of the mollusc decreased to 2360 specimens (in the eastern part of the estuary).

Marine euryhaline species occurred in the western and central parts of Schastje Bay. They are represented by the family Venerinidae and occurred at a salinity of 4.5-14.5°/oo. *Mytilus edulis* Linnaeus was found at 14.5-17.4°/oo, and *Onoba cingulata* (Middendorff), *Falsicingula elegans* Golikov & Kussakin and *Littorina kurila* Middendorff at 16.8°/oo.

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PUPILLOIDEA OF THE TALASS ALATAU MOUNTAINS

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Abstract

Among land Pulmonata inhabiting mountain ridges of South Kazakhstan, the superfamily Pupilloidea (Pupillidae, Vertiginidae, Orculidae, Valloniidae, Cionellidae) is the most abundant and widely distributed group. Members of the Pupilloidea differ in very small sizes and so very often remain beyond the vision of an investigator.

The work was conducted in the Talass Alatau mountains. It is a large rocky ridge of West Tien-Shan. Most of its northwestern region is occupied by the Aksu-Dzhabagly State Reserve. The mountain climate affects the vertical-zonal structure of vegetation and soil cover.

The fauna of land molluscs of the Talass Alatau mountains is poorly studied. The most complete data on the fauna are contained in the work by Khokhutkin (1976), who listed 10 species of land molluscs, five of them species of Pupilloidea, for the Aksu-Dzhabagly State Reserve.

As a result of treatment of our collections (April-May, 1977) and of the material preserved in the Institute of Zoology of the Academy of Sciences of Kazakh SSR, we established 11 species of molluscs belonging to the superfamily Pupilloidea. The list of members of the Pupilloidea from the Talass Alatau is given below, with an indication of their habitats.

Pupillidae: *Pupilla muscorum* (Linnaeus) – Kaindy trench, foothill steppe, Darbaza cordon, valley of the Zhetymsai River; *P. sterri* (Voith) – Kaindy trench, motley grassy meadow; *P. turcmenica* Boettger – valley of the Zhetymsai River; *P. bigranata* (Rossmaessler) – Ulken-Kaindy trench and Taldy-Bulak trench; *P. signata* (Mousson) – Kaindy trench, mountain steppe, Akbastau trench, valley of the Zhetimaai River.

Vertiginidae: *Columella columella* (Martens) – Bakhrau-Su trench, northern slope of the mountain, Aksu canyon, Kaindy trench, subalpine meadow, motley grassy meadow; *Truncatellina callicratis* (Sacchi) – everywhere.

Orculidae: *Sphyradium doliolum* (Bruguière) – Kaindy trench, Akbastau trench, valley of the Zhetymsai River.

Valloniidae: *Vallonia pulchella* (Müller), *V. costata* (Müller) – Kaindy trench, Akbastau trench, Bakhrau-Su trench; *V. excentrica* Sterki – Darbaz trench, valley of the Baldabrek River, valley of the Zhetymsai River.

Members of *Cionella* and of the genus *Vertigo*, which prefer most humid biotopes, were not recorded from dry slopes of the Talass Alatau.

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NEW DATA ON THE MOLLUSCS OF THE PAMIR

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Abstract

The Pamir, one of the highest uplands of the world, is situated mostly in the U.S.S.R. According to its relief, climate, soils, vegetative and animal world, the Pamir is divided into West Pamir (Bdakhshan) and East (Pamir proper).

Up to now, 24 species of land and freshwater molluscs were reported from the Pamir (Lindholm, 1931; Jankovskaya, 1965; Ursova & Dilman, 1971; Starobogatov, 1972): *Vallonia costata* (Müller), *V. pulchella* (Müller), *Cionella lubrica* (Müller), *Euconulus fulvus* (Müller), *Zonitoides nitidus* (Müller), *Orcula doliolum* (Bruguière), *Pupilla muscorum* (Linnaeus), *P. signata* (Mousson), *Columella columella* (Martens), *Subzebrinus albiplicatus* (Martens), *Chondrulopsina intumescens* (Martens), *Bradybaena perlucens* (Rosen), *Succinea putris* (Linnaeus), *Lymnaea stagnalis* (Linnaeus), *L. auricularia* (Linnaeus), *L. lagotis* Schranck, *L. bactriana* Hutton, *L. tenera* Küster, *Pyrgobaicalia*

aenigma Starobogatov, *Valvata pamirensis* Starobogatov, *Anisus convexiusculus* (Hutton), *A. ladacensis* Nevill, *Armiger annandalei* (Germain) and *Melanoides pamiricus* Lindholm.

Malacological material from various regions of Pamir was collected by the author in 1971, 1974 and 1976. In addition, collections of Drs. Gafurov, Akhrorov, Ergashboev, Egamov and Professor Gurvich were identified by the author. We wish to thank them for providing material.

As a result of treating the material, 45 species were recorded for Pamir, four of them being new for the fauna of the U.S.S.R.: *Anisus pancongensis* (Martens), *Lymnaea solidissima* Kobelt, *L. subdisjuncta* Nevill, *L. sirikulensis* Nevill; four species being new for Middle Asia: *L. tumida* Held, *L. fontinalis* (Studer), *Sphaerium corneum* (Linnaeus) and *Musculium creplini* (Dunker); two species being new for Tadzhikistan: *Succinella oblonga* (Draparnaud) and *Odhneripisidium stewarti* (Preston); 10 species being new for Pamir: *Pupilla asiatica* Möllendorf, *P.* cf. *muscorum* (Linnaeus), *Vallonia ladacensis* Nevill, *Caeciliodes acicula* (Müller), *Vitrina rugulosa* (Martens), *Phenacolimax annularis* (Studer), *Deroceras laeve* (Müller), *D. sturanyi* Simroth, *Parmacella aethiops* Westerlund and *Physella acuta* (Draparnaud); and two species being new to science: *Valvata gafurovi* Izzatullajev and *Melanoides shahdaraensis* Starobogatov & Izzatullajev.

The malacofauna of Pamir consists of two main ecological groups: land and freshwater mollusks. The distribution of the two groups in both the western and eastern parts of Pamir is quite irregular.

Twenty-three species of molluscs are recorded from West Pamir; of 13 species recorded for East Pamir (*Pupilla* cf. *muscorum* is the only land mollusc), 11 species are common for the whole of Pamir.

Among land molluscs, *Vallonia ladacensis* and *Succinella oblonga* are widely distributed throughout Pamir and are recorded from various altitudes. The former, however, lives in the limits of 2000-2200 to 4500-4600 m above sea level and the latter from 2400-3600 m above sea level and was not recorded from lower altitudes.

The above list of molluscs is undoubtedly not complete, but the data available enable us to draw some preliminary zoogeographical conclusions. Of the total number of species (46), 19 (41.3%) belong to widely distributed species (transholoarctic and transpalearctic), 19 (41.3%) are dendmics and subendemics, four (8.7%) are mountain Central Asiatic, three (6.8%) are European-Asiatic mountain and one (2.1%) (*Parmacella aethiops*) is considered to be a West Tien-Shan species.

It should be emphasized that, in a zoogeographical respect, the malacological fauna of Badakhshan differs from that of other parts of Pamir. The fauna of Badakhshan includes members of East-Asiatic (*Bradybaena perlucens*) and thermophilous Anterior Asiatic (*Leucozonella rufispira* (Martens)) species, but that they are missing in the fauna of Pamir proper apparently can be explained by cold climate and short summer, wide amplitudes of altitudes of East Pamir. Among freshwater molluscs of East Pamir, however, there occurred mountain Central Asiatic species which are absent from Badakhshan.

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LAND SNAILS OF KAZAKHSTAN AND ADJACENT TERRITORIES

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Abstract

Collections of molluscs preserved at the Institute of Zoology of Kazakh SSR and the author's collections conducted in the period of 1961-77 in Kazakhstan and Kirghizia served as the material for this work. Four natural or landscape zones (or belts) are distinguished within the territory of Kazakhstan.

Thirty-seven species of molluscs belonging to 16 genera and 13 families were found in the forest-steppe zone and forest-steppe altitude belt of the steppe zone. Best represented here are the species of the families Succineidae, Cionellidae, Vertiginidae, Pupillidae and Valloniidae. In a zoogeographical respect, the malacofauna of steppe landscapes of Kazakhstan is characterized by the prevalence of widely distributed boreal species. It is very similar to that of West-Siberian forest-steppe (Drozdov, 1965).

The malacofauna of Central Kazakhstan, which is concentrated in the steppe and semisteppe zones, is characterized by the prevalence of northern elements, nearly full absence of Middle Asiatic endemic groups of Limacidae (represented by one species), Bradybaenidae (represented by one xerophilous species) and by full absence of species of the family Enidae. In all, 27 species belonging to 12 genera and nine families were found.

Forty-two species belonging to 18 genera and 12 families were recorded from South Altai, which is situated in the steppe zone. The Tian-Shan mountain area situated in the desert zone is represented by three provinces: North Tien-Shan, South Tien-Shan and Central Tien-Shan.

The malacofauna of the North Tien-Shan province is rich and diverse. Members of 11 families and 18 genera inhabit the steppe belt of foothills, 10 families and 17 genera live in the forest-meadow-steppe middle-mountain belt and eight families and 10 genera of molluscs live in the Alpine meadow belt. The Alpine meadow belt is characterized by the prevalence of such cold-resistant mesophilous species as *Vertigo laevis* Uvalieva, *V. alpestris* (Alder), *Vitrina rugulosa* Martens, *Succinea altaica* Martens, *Bradybaena plectotropis phaeozona* (Martens) and *Angiomphalia exasperata* Schileyko & Uvalieva.

Molluscs of 10 families and 12 genera are recorded from Central Tien-Shan province, from forest-meadow and steppe middle-mountain belt; 13 families and 16 genera were recorded from Alpine-plateau meadow-steppe and steppe belt and four families from nival belt. Species of the superfamily Pupilloidea and the families Bradybaenidae, Hygromiidae and Enidae are most abundant. In nival belt, in areas more than 4,000 m above sea level (upper reaches of the Myn-Turuk and Sary-Dzhaz rivers, Koksai trench), species of *Pupilla*, *Columella* and *Vallonia* were found in great abundance. On bare rocks (90 m in height and 200 m in width), there are many specimens of *Succinea altaica martensiana* Nevill. They feed, apparently, on algae, fungi, actinomicetes and bacteria, which are so abundant on the surface of rocks.

In southwestern Tien-Shan province, there are members of 23 genera of 16 families of land molluscs. Members of 21 genera of 13 families occur in the meadow-steppe belt (1200-2000 m), members of 10 genera and seven families occur in the Subalpine belt (2000-3000 m) and five families of molluscs occur in the Alpine belt (over 3000 m). Most rich in species is the meadow-steppe belt. Here members of the families Pupillidae, Orculidae, Enidae and Hygromiidae occur.

As one can see from the above data, the specific complex of molluscs in various physical-geographical regions of Tien-Shan is different. This depends on the extension of ridges, steepness of slopes and substratum and on various types of soil and vegetation. In a zoogeographical respect, malacofauna of mountain systems of Tien-Shan is characterized by a combination of elements of Anterior Asiatic, boreal and Central Asiatic origin and by a considerable level of endemism.

Middle Asiatic species are most abundant on all mountain ridges of Tien-Shan. Members of the families Bradybaenidae, Hygromiidae, Pupilloidea and Enidae are widely represented.

Recently, seven species new to science have been described from plain and mountain parts of Kazakhstan; new species of the genera *Pupilla, Columella, Vallonia* and *Monachoides* have been found and described. Also, in some greenhouses and on fields of Zailijsky Alatau, there were found *Deroceras caucasicum* (Simroth), *D. sturanyi* (Simroth), *D. reticulatum* (Müller) and *Oxychilus translucidus* (Mortillet) brought from the Caucasus and European part of the U.S.S.R.

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THE POSSIBILITY OF AGE DETERMINATION IN *DREISSENA POLYMORPHA* BY THE STRUCTURE OF THE SEPTAL SURFACE

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Abstract

When determining the age of *Dreissena polymorpha* (Pallas) by means of calculation of annual (seasonal) rings on a shell's valves, errors can be possible, because some other rings are formed on the shell depending on the physiological state of the individual, temporary drying, abrupt fluctuations in the temperature and oxygen regime of the environment, various injuries, diseases, etc.

In *Dreissena*, the septum can serve as an independent registrating structure. It represents a barrier in the interior part of each wall of the shell to which the anterior adductor is attached (the impression occupies nearly all of the surface of the septum). When examining the impression under a microscope, it is clearly seen that on it there are broad light and narrow dark strips. The surface is sculptured: narrow strips are somewhat depressed and are more transparent than are broad ones. For studying the structure of the impression of the muscle, the latter is removed by the scalpel, but its remains prevent us from examining the septum. To remove the remains, Spiridonov's (1975) technique can be used, but, to avoid the disturbance of the muscle's impression relief, a further treatment of the shell with NaCl after boiling it in 5% NaCl should not be done.

Results of calculation of the strips on the septum coincide in most cases with results of calculations of seasonal rings on the shell. Thus, in molluscs up to the age of 3+, only two of 70 calculations raised doubts. In older individuals, the disagreement in calculations was no more than 3.5-4.0%. Thus, the structure of the relief of the septum can be used for determining the age of *Dreissena* by seasonal rings on the shell, but at the same time it can be used quite independently.

The septum is formed somewhat later than the shell. This occurs at the stage of postveliger, when the mollusc reaches the size of 0.6-0.7 mm. So it is quite natural that changes proceeding earlier in the structure of the septum remain unfixed. The septum responds to the changes of seasonal character; this registrating structure is far less sensitive to intraseasonal changes.

The structure of the relief of the septum is quite distinct in some individuals and is less distinct in others, which, from our point of view, is associated with ecological differences. In very polluted habitats, at great depths and slow water currents, the relief of the septum is indistinct. This peculiarity can be used, apparently, in establishing the belonging of a population of *Dreissena* to definite elementary groupings.

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EXTENSION OF THE DISTRIBUTION OF *DREISSENA BUGENSIS*

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Abstract

Invertebrates of the Ponto-Caspian complex play an important part in the formation of the fauna of the Dnieper and its water reservoirs. In addition to many species of crustaceans occurring here, molluscs also have become widely distributed in this region, *Dreissena* in particular. Before the impoundment of the river, the Dnieper-Bug liman and lower reaches of the Dnieper were the main localization sites of *D. bugensis* (Andrusov).

In Zaporozhje water reservoir, which was constructed in 1931-34, *Dreissena bugensis* was found in 1941. After

reconstruction of Zaporozhje hydroelectric power station in 1947, which was destroyed during World War II, the species got favorable conditions for further spread up the Dnieper, For 5-6 years, it occupied Dnieprodzerzhinsk water reservoir, which was filled in 1963-64, and was found in great abundance down the Kremenchug water reservoir dam constructed in 1960. At the end of the 1960s, *D. bugensis* was far more abundant than was *D. polymorpha* (Pallas) (85-90%; total biomass, 4-6 kg/m^2) in most parts of the Dnieprodzerzhinsk water reservoir.

In the Kakhovka water reservoir, the distribution of *Dreissena bugensis* began just after its construction (1956), but its mass spread here was noted only in 1963, mainly in the lower part of the reservoir. Here, *D. bugensis* nearly forced *D. polymorpha* out and began to occupy the upper parts of the reservoir. In 1977, 80-90% of the *Dreissena* colonies in this part of the reservoir consisted for *D. bugensis*. The coenosis of "*D. polymorpha*" with its variants, which at the end of the 1960s occurred mainly in this part of the reservoir, does not exist now.

For the past years, there was noted a wide spread of *Dreissena bugensis* along the canals of the Ukraine. This spread is provided by the outflow of *Dreissena* veligers along the system of canals.

In the first years of the existence of the Kremenchug water reservoir, only *Dreissena polymorpha* was found there. Somewhat later, in the lower part of the reservoir and then in its central part, the distribution of *D. bugensis* began. In 1966-67, this species was absent from the group of dominant species, but at the beginning of the 1970s it prevailed already over *D. polymorpha*, especially in the lower part of the reservoir. It should be noted that in the shallow zone of the reservoir, in its lower and middle parts, *D. bugensis* was found only in 1974 (30-40% of the total number of both species).

In the youngest Kanev water reservoir, *Dreissena bugensis* was recorded by Pidgaiko in 1972. As far as this species was not found earlier above the water level of the Kremenchug reservoir, it can be suggested that it was introduced into the region together with fowlings from lower parts of the Dnieper.

In 1977, *Dreissena bugensis* was found in the shallow zone of the middle part of the Kiev water reservoir. Only yearlings were found in samples, but in the lower part of the reservoir individuals of older ages, apparently, occur.

Under conditions prevailing in the system of the Dnieper water reservoirs, the hypothesis of Zhuravel on a possible spread of *Dreissena bugensis* through the Pripiat and Neman to the basin of the Baltic has become quite urgent. The distribution of molluscs in the Pripiat is little possible, since waters of this river are saturated with huminous substances and have low indices of hardness and pH. They can penetrate waters of Pribaltic quite often with water transport.

A wide distribution of *Dreissena bugensis* in the Dnieper drainage was caused by a strong antropogenous effect upon the ecosystem of the river (impoundment of the river and creation of a system of water reservoirs). This process was accompanied by the formation of environmental conditions favorable for the development of *D. bugensis* (fall in the current velocity, silting of the bottom). The distribution of *D. bugensis* also can be favored by the intensive navigation on the Dnieper.

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ON THE APPLICABILITY OF THE SPECIFICITY OF TREMATODE PARASITES TO THE TAXONOMY OF THE LYMNAEIDAE

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Abstract

Specificity is understood most often as an association of parasites with a definite species of a group of species of animal hosts. This association and the adaptation connected with it are regarded as a consequence of long evolution of host-parasite relationships. The earlier they are formed, the more narrow is the specificity of the parasite in relation to the host.

A necessary link in the life cycle of trematodes is a mollusc. It serves as a first intermediate host for all species of trematodes, regardless of which animal plays a part of the second or definitive host. Of 4,000 species of trematodes, only two species have polychaetes as the first intermediate host (Ginetzinskaya, 1968). This is indicative of the stability of relations between trematodes and the first intermediate host and serves as evidence of the priority of molluscs in phylogenesis of trematodes. It is quite true that the host is as specific to the parasite as the parasite is to the host (Dogiel, 1962). Proceeding from this, we can draw a conclusion on the possibility of using the criterion of specificity of trematodes in the taxonomy of molluscs. In this respect, Kendall's (1965) statement that a parasite, apparently, distinguishes species of molluscs with more confidence than any taxonomist is noteworthy. As our studies have shown, this statement is not without reason.

The recent stage of malacology is characterized by a revision of an earlier constructed system, of groups in particular, which are of great parasitological importance. It seems quite reasonable to conduct in the course of such revision checking on newly erected species from a parasitological point of view. With such an approach, we solve at the same time a problem of correctness of establishment of new species of molluscs as far as the degree of susceptibility to infection emphasizes its biological peculiarity that is of interest in a taxonomic respect.

The criterion of specificity of helminths in relation to molluscs, the first intermediate hosts of trematodes, was used by us for analysis of specific distinction of molluscs of the species *Lymnaea (Radix) ovata* Draparnaud. For this purpose, the trematode *Fasciola gigantica* (Cobb), which displays a rather narrow specificity in relation to some lymnaeids of the subgenus *Radix*, was chosen.

In numerous experiments, we failed to infect adult molluscs of the *Lymnaea (Radix) peregra* form with miracidia of *Fasciola gigantica*, while molluscs of the *L. (R.) ovata* form were easily infected and a lot of rediae and cercaria of this helminth developed in them. Based on this, we conducted an experiment of comparative infection of molluscs of *L. (R.) peregra* and *L. (R.) ovata* forms with miracidia of *F. gigantica*. In the process of infection, there was noted an active and mass invasion of miracidia only into *L. (R.) ovata*.

In 40 days after infection in an artificial biotope, where *Lymnaea (Radix) ovata* were maintained, the first adolescaria were recorded. In another biotope, however, where *L. (R.) peregra* were maintained, no adolescaria were found.

The final control of the experiment was conducted in 12 days. Eighteen *Lymnaea (Radix) peregra* and 10 *L. (R.) ovata* were examined. Among *L. (R.) peregra*, there were no infected individuals, while of 10 examined *L. (R.) ovata*, nine were infected with rediae and cercariae of *Fasciola gigantica*.

Thus, this experiment has determined distinct differences in the susceptibility of *Lymnaea (Radix) ovata* and *L. (R.) peregra* to infection with *Fasciola gigantica* that is convincing evidence of specific distinction of these forms.

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THE ROLE OF LAND MOLLUSCS IN THE LIFE-CYCLES OF HELMINTHS FROM KAZAKHSTAN

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Abstract

This work is a result of a ten-year study of land molluscs as intermediate hosts of helminths. The author's own material was used, which was obtained during the dissection of over 35,000 specimens belonging to 22 species and 10 families: Succineidae, Limacidae, Ariophantidae, Bradybaenidae, Hygromiidae, Endodontidae, Pupillidae, Valloniidae, Vitrinidae and Zonitidae. The collection of land molluscs was conducted mainly in the mountains of Kazakhstan-Zailijsky, Kungei and Talass Alatau and in South Altai. The work on the identification of *Leucochloridium* was conducted on the shore of Lake Balkhash and lakes of Kokchetav, Tzelinograd and Karaganda districts.

Twenty-seven species of helminths were found in molluscs (24 species of trematodes, two species of cestodes and one species of nematode). In some species mermithids were found, the specific composition of which is not yet established. Most species of helminths belong to the superfamily Brachylaimoidea, in particular to the following families: Brachylaimidae, Leucochloridiidae and Hasstilesiidae (*Brachylaimus alequans* (Loess), *B. spinulosus* (Hoffmann), *B. recurvus* (Dujardin), *B. nicolli* (Wittenberg), *B. fuscatus* (Rudolphi), *Brachylaimus* sp., *Postharmostomum gallinum* Wittenberg, *P. commutatum* (Diesrug), *Pseudoleucochloridium* sp., *Leucochloridium paradoxum* Carus, *L. problematicum* Majath, *L. vogtianum* Baudon, *L. kazachstanicum* (Butenko), *Leucochloridium* sp., *Hasstilesia ovis* (Orloff, Ersnoff, Badanin), *H. ochotonae* Gvosdev). Five species of dictocoelids were found: *Dicrocoelium lanceatum*, *Eurytrema pancreaticum* (Jauson), *Corrigia corrigia* (Braun) and Dicrocoeliidae (2 species). In addition, there were found: Eucotylidae (*Tamerlania* sp.) and Microphallidae (*Microphallus helicicola* Soboleva), two species of cestodes of the family Dilepididae and one species of nematode of the family Protostrongylidae.

The infection of land molluscs with parthenites and larvae of trematodes is not the same everywhere and is of nidal character. The highest infection rate of molluscs was observed in humid trenches, on the slopes of the northern exposition, on shores of brooks and mountain rivers. It depends as well on definitive hosts, abundance of molluscs and ecological conditions which promote the circulation of infection. The nidi of brachylaimosis, hasstilesiosis and postharmostosiosis are associated with steppe, forest and subalpian belts, while nidi of dicrocoelosis and eurytremosis are associated with a steppe belt in general. Eucotylids were found in a forest belt and macrophallids in both steppe and subalpian belts.

Molluscs of the families Limacidae, Ariophantidae, Bradybaenidae and Hygromiidae play an important part in the distribution of brachylaimids in rodents and birds, including Galliformes.

Trematodes of the family Hasstilesiidae are associated in their development with molluscs of Vertiginidae, Pupillidae and Valloniidae, and trematodes of Leucochloridiidae with Succineidae. Dicrocoeliids develop in 15 species and subspecies of five families. But trematodes of some genera are adapted to a more narrow range of molluscs, e.g., *Eurytrema* develop only in the Bradybaenidae. Larvae of *Tamerlania* sp. were found in *Succinea*, and *Microphallus helicicola* were found in *Bradybaena*. Larvae of cestodes were found in *Succinea altaica* Martens, *Macrochlamys kasachstani* Tzvetkov, *M. schmidti* Branczik and *Limax turkestanus* Simroth. The latter was infected with nematodes as well. Mermithides were recorded from *S. altaica*, *B. phacozona* (Martens) and *Jaminia potaniniana* (Ancey).

Therefore, helminths have differently expressed specificity to land molluscs. As a rule, species which undergo complex morpho-physiological changes in the intermediate host have a narrow specificity. Of the above trematodes, it is mostly expressed in leucochloridians and hasstilesians and for nematodes it is expressed in protostrongylids. Brachylaimids and dicrocoelids, which represent most flourishing groups of trematodes occupying new hosts, have a wide specificity to land molluscs.

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SEASONAL DYNAMICS OF THE INFECTION OF *LITTORINA SAXATILIS* WITH PARTHENITES OF *MICROPHALLUS PYGMAEUS* (TREMATODA: MICROPHALLIDAE) IN THE YARNYSHNAYA INLET (EASTERN MURMANSK COAST)

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Abstract

The life cycle of *Microphallus pygmaeus* (Levinsen) has one intermediate host, a mollusc (primarily members of the genus *Littorina*) in which parthenites and metacercariae develop (Belopolskaya, 1949). Daughter sporocysts

destroy the hypobranchial gland and gonad and cause sexual sterility of molluscs. *Somateria mollissima* (Linnaeus) is a definitive host of the parasite.

Seasonal dynamics of the infection of molluscs with *Microphallus pygmaeus* was studied on both the Barents (Chubrik, 1966; Podlipaev, 1975) and the White seas (Zelikman, 1966). These authors, however, considered only total infection; separate registration of parthenites according to their ages was not conducted. Due to this, there was no complete picture of seasonal dynamics of the development of *M. pygmaeus*.

The work was conducted at the Murmansk Marine Biological Institute (Dalnie Zelentsy) in July-October 1977 and February 1978. Material was collected in the intertidal zone and innermost part of the Yarnyshnaya Inlet. Each sample consisted of 200-400 specimens of *Littorina saxatilis*. Daughter sporocysts of *Microphallus pygmaeus* were arranged into three age groups: 1) sporocysts containing embryonal spheres and embryos of cercariae; 2) sporocysts containing young metacercariae at different developmental stages; 3) mature sporocysts containing invasional metacercariae.

Early in August, 44% of investigated molluscs were infected with *Microphallus pygmaeus*. Six percent of the *Littorina* were infected with sporocysts containing embryos of cercariae, 17% with sporocysts of middle ages, and 21% with mature sporocysts. By the middle of September, the total infection of *L. saxatilis* with parthenites of *M. pygmaeus* was 56%: sporocysts with embryos of cercariae amounted to 3% and molluscs infected with mature sporocysts to 37%. Their number increases because middle-aged August sporocysts have completed their development by this time, and August sporocysts with embryos of cercariae turn into middle-aged sporocysts. On this basis, we expected that the infection of molluscs with middle-aged sporocysts will be in September of the same order as the infection with sporocysts containing embryos of cercariae in August (6%). However, in September, *Littorina* infected with middle-aged sporocysts amounted to 16%. Such a discrepancy in data depends apparently on the fact that the earliest stages of the embryonal development of *M. pygmaeus* parthenites cannot virtually be counted due to their small sizes.

In the second half of October, the total percent of infection of *Littorina saxatilis* decreased to 51%. Mature sporocysts amounted to 36%, middle-aged sporocysts to 12%, and sporocysts with embryos of cercariae to 3%. Proceeding from the percent number of molluscs infected with mature and middle-aged sporocysts in September, we expected a considerably greater infection of *Littorina* with mature sporocysts in October. But from the middle of September, weather conditions in the investigated region changed for the worse. With the coming of unfavorable conditions, sick animals die, and that, apparently, can explain a lower infection with mature sporocysts in October in comparison with the expected one.

In February, the total infection of molluscs amounted to 27% (molluscs infected with sporocysts containing embryos of cercariae amounted to 13%, with middle-aged sporocysts 3% and with mature sporocysts 11%). A considerable decrease in the infection with mature sporocysts is, apparently, connected with mortality of molluscs. It should be noted that individuals infected with mature sporocysts die first of all. February mature sporocysts apparently represent October middle-aged sporocysts which reached the invasional state.

The first mass infection of *Littorina saxatilis* may take place only in April-May (spring flight of eider). At this time in the region of investigations, maximum quantity of eider is observed and *Littorina*, which in winter during low tide hide themselves under stones, pass to an active mode of life. By the end of July or the beginning of August, mature sporocysts appear in molluscs, which, apparently, were infected at the beginning or middle of April. In molluscs, which were infected later, there are middle-aged sporocysts and sporocysts with embryos of cercariae. In September, the spring infection is represented by mature sporocysts and partly by middle-aged sporocysts. Most molluscs infected with middle-aged sporocysts and all molluscs infected with sporocysts with embryos of cercariae were infected in summer (broods of eider). October mature sporocysts are a result of both spring and summer infection. Summer infection is represented in October as well by middle-aged sporocysts and by sporocysts with embryos of cercariae. In autumn, mass infection of *Littorina* (autumn flight of eider) takes place that is associated with high extensity of infection with sporocysts containing embryos of cercariae in February. Summer and partly autumn infection is represented in February by mature sporocysts. February sporocysts with embryos of cercariae reach the invasional state most likely by April (spring flight of eider). Thus, there are close links between the dynamics of a parasite's development and ecology of definitive and intermediate hosts that points to a high degree of specialization of host-parasite relationships in the species *Microphallus pygmaeus*.

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THE PRINCIPAL RESULTS AND PERSPECTIVES OF THE STUDY OF HELMINTH FAUNA OF THE ATLANTIC CEPHALOPODS

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Abstract

The present report is based on results of helminthological investigations of Atlantic cephalopods conducted by the author in 1973-76 and on the analysis of available literature.

In 30 species of cephalopods, helminths of five classes were found: trematodes (18 species), cestodes (21), monogeneans (1), acanthocephalans (2) and nematodes (8). Most species are represented by larval forms: metacercarians (trematodes), pleurocercoids (cestodes), second and third stage larvae (nematodes). Trematodes are represented by juvenile and mature forms and acanthocephalans by only mature ones.

For most helminths that have been found, cephalopods serve as additional or reservoir hosts, in some cases playing the part of definitive hosts. Cestodes, which parasitize cephalopods, accomplish their development in Chondrostei, and nematodes of the genera *Anisakis* and *Terranova* develop in marine mammals.

The infection of cephalopods is carried out by means of food. Their abundance, great variety and relative stability

of food links have stipulated a role of cephalopods as a main link between first and second intermediate and definitive hosts in life cycles of helminths parasitic in them.

Age changes in tropic links of cephalopods undoubtedly affect their parasite fauna. The indices of extent and intensity of infection increase, as a rule, with increasing size of squids. Maximum infection with didimosoid metacercariae, however, was recorded in squids reaching a size of 10-15 cm.

The infection rate of cephalopods depends on the region of investigation and on the species of a host. Thus, of 617 squids of *Todaropsis eblanae* (Ball) off the coast of Northwest Africa, none was infected, while this species in the region of Southwest Africa was infected at a rate of 13.5%.

Excluding *Isancistrum loliginis* Beauchamp parasitic in *Loligo vulgaris* Lamarck, all other helminths have a wide specificity and use Chondrostei as intermediate hosts at the same developmental stages. The presence of "fish helminths" in cephalopods is connected with an ecological proximity of cephalopods and Chondrostei. In other words, helminth fauna of cephalopods is of secondary character.

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A VARIANT OF SYMPATRIC SPECIATION IN SNAILS

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Abstract

At present, dextral and sinistral races of snails are considered to be "good species" or species in *statu nascendi* (Matiokin & Ivankova, 1975, Schileyko, 1975). It is known (Boycott et al., 1930, and others) that the direction of coiling of the shell is a character with monogenic diallelic inheritance. In some groups (Lymnaeidae), right coiling is dominant, while in the others (Partulidae) left coiling is dominant. The display of the mutant allele in a homozygote proceeds with phenotypical delay — irrespective of its genotype, the progeny has coiling corresponding to the maternal genotype (=maternal heredity). In the case of dominant dextrality, the appearance of many sinistral individuals is possible due to the crossing of a phenotypically dextral mother which is homozygous by a mutant allele, with any partner.

Reversion of coiling results in a complete or partial isolation of mutants. In some land molluscs, crossing is either mechanically impossible or seldom accomplished (Clarke & Murray, 1969, and others); for *Lymnaea peregra* (Müller) crossing is possible, but in hybrid lines there are many conchological monstrosities and high embryonic mortality (Boycott et al., 1930, and others). Thus, mutation of one gene gives rise to homozygous mutants, which are reproductively isolated from an ancestral population. Differentiation of populations on the basis of this mutation can be considered momentary sympatric speciation.

Mutation of the reverse coiling can arise in any population on account of spontaneous mutagenesis and exists indefinitely in the heterozygous state, not displaying itself phenotypically. Low mobility of most snails provides a possibility of inbreeding that easily can result in the appearance of individuals which are homozygous for a mutant allele. Specific mechanism of inheritance as was mentioned above determines a simultaneous appearance of several individuals of mutant phenotype in a population. These individuals will be reproductively isolated from an ancestral population, but reproducing "in themselves" they can form a stable colony. Under favorable conditions, their area can be enlarged and they thus form a geographic population isolated completely from the ancestral species.

Such a scheme is confirmed by numerous examples of various stages in differentiation of dextral and sinistral races: from small colonies to large geographic races in contact zones where conchological monsters can be found. It is noteworthy that sinistral species and races occur, with few exceptions, only in groups with a pronounced limitation of distributive ability: hermaphroditic Pulmonata and marine forms which do not have a planctonic larva.

Four stages can be distinguished in the above process of speciation: 1) latent existence of mutations; 2) appearance of phenotypically mutant forms; 3) formation of a stable colony; 4) broadening of the area and formation of populations and geographic races. This scheme agrees with that of neoformogenic speciation (Zavadsky, 1968) and can be considered universal for an instant sympatric speciation.

It should be noted that, during the above processes, polytypic speciation or the formation of several species undoubtedly can take place on account of simultaneous appearance of populations of sinistral forms in various parts of the area of the ancestral species. This character makes the determination of taxonomic status of sinistral and dextral forms of the same species difficult, but in general the stable geographic populations with different spirality should be considered distinct species.

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NEWS AND ANNOUNCEMENTS

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UNITAS MALACOLOGICA. – *Unitas Malacologica* is an international organization of malacologists and malacological societies whose goal is to support malacological research throughout the world and to regularly organize international malacological Congresses. The originally European society, founded in 1962 in London, was changed into a more broadly international organization in 1977 and now has more than 200 members all over the world. Its legal domicile is Basle, Switzerland. The annual subscription is 20 Swiss francs. This membership fee includes the Proceedings of the Congresses, held every third year. The last Congress was held in Budapest, Hungary, in 1983. The next International Malacological Congress will be held in Edinburgh, Scotland, in 1986.

Questions and applications with respect to membership should be sent to the Secretary, Dr. Oliver E. Paget, Natural History Museum, Burgring 7, A-1014 Vienna, Austria.

SOCIEDAD ESPAÑOLA DE MALACOLOGÍA. – The Sociedad Española de Malacología is open to anyone throughout the world who is interested in malacology. The scientific publication of the Society is *Iberus* (see p. 152, *Malacol. Rev.*, Vol. 16). Personal memberships cost US$23.00 per annum (plus an initial fee of US$7.50). Back issues of the journal (Vols. 1 and 2) can be purchased at US$15.00. Institution membership is US$35.00. Institutions can purchase back issues of *Iberus* for US$27.00. Fees may be paid by International Postal Money Order to C/C Postal 4.351.669, Sociedad Española de Malacología, Caja Postal de Ahorros. The address of the Society is: Sociedad Española de Malacología, Museo Nacional de Ciencias Naturales, Paseo de la Castellana, 80, Madrid-6, Spain.

THE INSTITUTE OF MALACOLOGY held its annual meeting on 9 August 1983 in Seattle, Washington, U.S.A. Members present were S.K. Wu (President), J.B. Burch, Melbourne R. Carriker, George M. Davis, Robert Robertson and Clyde F.E. Roper. One significant decision, not unanimous, but following the wishes of the Co-Editors-in-Chief, was to discontinue the publication for *Unitas* of the Proceedings of the International Malacological Congresses. Henceforth, *Malacologia* will cease this long-standing affiliation with *Unitas* and the Malacological Congresses. However, the possibility was left open that *Malacologia* may on occasion in the future publish special symposia of the Congresses.

THE EIGHTH INTERNATIONAL MALACOLOGICAL CONGRESS was held in Budapest, Hungary, 28 August-3 September 1983, under the direction of the President, László Pintér. In addition to contributed papers and posters, three special colloquia were organized by the Congress: Quaternary malacology and faunal history, Sphaeriidae, and non-marine molluscan biogeography and zoogeography. The Proceedings of the Eighth International Malacological Congress will not published in *Malacologia*, thus breaking a long-standing tradition. To fill this need, the Hungarian Academy of Science has agreed to publish the Proceedings of the Eighth Congress. Anyone wishing further information should contact Dr. László Pintér, Hungarian Natural History Museum, Baross utca 13, H-1088 Budapest, Hungary.

MEETING OF THE SOCIETY FOR EXPERIMENTAL AND DESCRIPTIVE MALACOLOGY. – The 1984 annual business meeting of the Society for Experimental and Descriptive Malacology will be held in July 1984 in Ann Arbor, Michigan, U.S.A.

THE 1984 ANNUAL MEETING OF THE INSTITUTE OF MALACOLOGY will be held in Norfolk, Virginia, U.S.A., at 3:00 P.M. on 22 July 1984, just prior to the annual meeting of the American Malacological Union. For further details, contact Dr. S.K. Wu, President of the Institute of Malacology, c/o University of Colorado Museum, Campus Box 15, Hunter Building, Boulder, Colorado 80309, U.S.A.

THE NINTH INTERNATIONAL MALACOLOGICAL CONGRESS, sponsored by the *Unitas Malacologica*, will be held in Edinburgh, Scotland, in September 1986. For further information, please contact the current President of *Unitas Malacologica*, Dr. David Heppell, The Royal Scottish Museum, Chambers Street, Edinburgh EH1 1JF, Scotland.

OSHA EXEMPTS EDUCATIONAL/SCIENTIFIC DIVERS. – After six years of work by members of the American Academy of Underwater Sciences and the U.S. Occupational Safety and Health Administration, an exemption for Educational/Scientific Divers to the federal regulations covering Commercial Divers (29 CFR Part 1910) has been granted.

To operate under the exemption OSHA requires that, 'Scientific diving be under the direction and control of a Diving Program utilizing a Diving Safety Manual and a Diving Control Board meeting certain specified criteria.'

The text of the exemption is contained in the Federal Register / Vol. 47, No. 228 / Friday, November 26, 1982 / Rules and Regulations / pages 53357 to 53365. Those requiring more information should contact the Secretary of the A.A.U.S., Phillip Sharkey, Graduate School of Oceanography, Narragansett, Rhode Island 02882, U.S.A., or call him at (401) 792-2980.

MALACOLOGICAL REVIEW, SUPPLEMENTS 1, 2 AND 3. – Supplements 1, 2 and 3 are available from *Malacological Review* at the prices given below. They can be ordered from *Malacological Review*, P.O. Box 637, Niwot, Colorado 80544, U.S.A.

Supplement 1. *Freshwater snails of Taiwan (Formosa)*, by Gary L. Pace. This illustrated monographic study deals with the identification, classification, distribution, zoogeographic affinities and parasitological importance of thirty-nine species of Formosan freshwater gastropod mollusks. US$20.00, postpaid.

Supplement 2. *The Mekong schistosome*, J.I. Bruce, S. Sornmani, H.L. Asch & K.A. Crawford, Editors. This publication is a monograph on the newly discovered human blood fluke, *Schistosoma mekongi*, and its unusual molluscan host, *Tricula aperta*. In addition to details on the parasite, this book presents various studies on the snail intermediate host, including its anatomy, systematic and zoogeographic relationships, evolution, habitats and bionomics, laboratory maintenance and culture, susceptibility to the parasite, effect of the parasite on the snail, the snails' role in disease transmission, and sensitivity of the snails to molluscicides. US$26.00, postpaid.

Supplement 3. *A dissection guide, field and laboratory manual for the introduced bivalve* Corbicula fluminea, by Joseph C. Britton & Brian Morton. This manual is a timely publication on *Corbicula* in North America. It documents the clam's past history and spread on this continent, and deals with its taxonomy, nomenclature, ecology, functional morphology and physiology. Various laboratory exercises are presented whereby these numerous and common clams can be used to demonstrate aspects of molluscan bivalve biology. US$16.00, postpaid.

NORTH AMERICAN FRESHWATER SNAILS. – The final part of a three-part series on *North American freshwater snails* will be released soon: *Introduction, systematics, nomenclature, identification, habitats, ecology and distribution*, by J.B. Burch, 80 pp., 20 figs., 1984. The first two parts are: *Species list, ranges and illustrations*, by J.B. Burch & John L. Tottenham, 135 pp., 751 figs., 1980; *Identification keys, generic synonymy, supplemental notes, glossary, references and index*, by J.B. Burch, 149 pp., 280 figs., 1982.

All three parts can be ordered from *Malacological Review*, P.O. Box 637, Niwot, Colorado 80544, U.S.A. Their prices are US$12.00, $20.00 and $25.00, respectively, postpaid.

MALACOLOGY IN KOREA. – There has been an increasing interest in mollusks in Korea – an interest in their basic biology and taxonomy, in their relation to aquatic pollution, in their status as intermediate hosts of human and veterinary parasites, as benthic organisms, as fossils, etc. These interests led to a desire to form a scientific society of malacologists, which resulted in a number of informal meetings being held during 1983, culminating in more formal organizational meetings on 13 and 19 December 1983. Additional meetings will be held in January and March 1984. It is expected that the outcome of these deliberations will be the formation of a Society of Korean Malacologists.

MALACOLOGIST POSITION OPEN IN THE SMITHSONIAN INSTITUTION. – A malacologist position at entry level GS-11/12 ($25,366-$30,402) is available in the Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., for a person specializing in opisthobranchs, bivalves or pulmonates. Applications should be submitted by 15 April 1984. For further information, contact Dr. Clyde F.E. Roper, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., 20560, U.S.A. [telephone no. (202) 357-2030].

IMPROVED CURRENT MALACOLOGICAL LITERATURE COVERAGE. – *Malacological Review* plans to reorganize and increase the size of its "Publications" section, offering a better review of current malacological literature. The larger size of the journal will make publication more expensive and, to offset this, there will be a small increase in subscription price. The new subscription prices will be US$15.00 for private individuals in the U.S., US$17.00 for private individuals in any other country, US$27.00 for U.S. institutions and US$30.00 for foreign institutions.

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CONTENTS OF CURRENT SERIAL PUBLICATIONS ON MOLLUSKS

The contents of current malacological serial publications, as shown by their tables of contents, are herewith reproduced as a service to our readers. The publications are listed in alphabetical order. Also listed are the locations of the editorial offices. Those publications that do not have their contents printed in this current issue of *Malacological Review* are marked by an asterisk in the right-hand column below; contents of these publications will be included in future issues of *Malacological Review*. Henceforth, serials which are newsletters of malacological societies will be treated separately from malacological journals. The first newsletter contents section will appear in Vol. 18 of *Malacological Review*. Societies wishing to be included in this coverage should send their newsletters to *Malacological Review* (P. O. Box 2749, Ann Arbor, Michigan 48106, U.S.A.).

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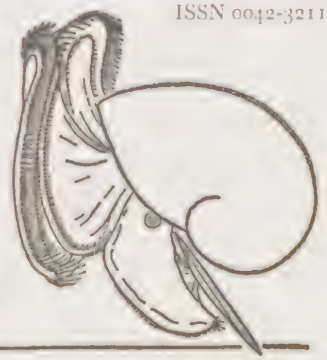

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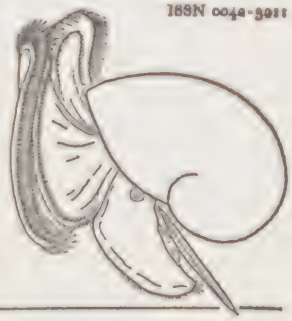

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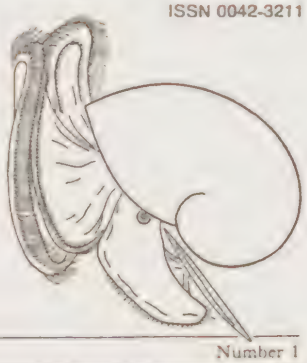

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MALACOLOGICAL ARTICLES IN SOME CURRENT BIOLOGICAL AND PALEONTOLOGICAL SERIAL PUBLICATIONS

Since its initiation in 1968, *Malacological Review* has attempted to serve as a bibliographic source for scientific articles on mollusks. Pursuant to this aim, the journal regularly has reproduced the tables of contents of all current malacological journals in its section "Contents of current serial publications on mollusks", and it has listed under "Publications" current books, monographs and research and original articles on mollusks that have been brought to the editors' attention. *Malacological Review* is now adding another bibliographic feature – listing all "Malacological articles in some current biological and paleontological serial publications". In the current issue of *Malacological Review*, all previous articles on mollusks that have appeared in seven publication series are listed below: 1) *Proceedings of the Biological Society of Washington*, 2) *Occasional Papers of the Museum of Zoology, The University of Michigan*, 3) *Miscellaneous Publications of the Museum of Zoology, The University of Michigan*, 4) Michigan Handbook Series, Museum of Zoology, The University of Michigan, 5) Circular Series, Museum of Zoology, The University of Michigan, 6) *Contributions in Science, Natural History Museum of Los Angeles County, California*, and 7) *Smithsonian Contributions to Zoology*. The Editor for this series is Walter E. Sage, III.

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Errata, Vol. 16

p. 29: The shells in Fig. 1 are enlarged x 3.8.

p. 84, line 9: $\sqrt{FG^2} + \overline{FH}^2$ should read $\sqrt{\overline{FG}^2 + \overline{FH}^2}$.

p. 110: The figure numbers by the shells of Figs. 21 and 22 are reversed. *Nerita* is on the left and *Clithon* is on the right.

p. 135, line 16: p. 000 should read p. 152.

p. 212, line 2: 1978 should read 1968.

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